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TEMPERATURE COEFFICIENTS IN PLANT GEOGRAPHY AND CLIMATOLOGY[1]

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(WITH THREE FIGURES)

Introduction

Plant geographers and climatologists have long been convinced that temperature is one of the most important of the conditions governing the distribution of plants and animals, but very little has as yet been accomplished toward finding out what sort of quantitative relations may exist between the nature of floral and faunal associations and the temperature conditions that are geographically concomitant therewith. The progress of descriptive ecology has shown clearly enough that these associations have their geographical limits, and increased accuracy of description has developed hand in hand with the idea that association boundaries must be considered as peripheries of certain complexes of environmental conditions. It is common, in recent papers upon plant and animal geography, to give considerable attention to descriptions of the climatic complexes which characterize the vegetational or faunal areas dealt with, but such description of climates has thus far usually consisted in the mere quotation or compilation of various meteorological data. In order to correlate these data with physiological phenomena, in such a way as to throw light upon the effective climatic

[1] Botanical contribution from the Johns Hopkins University, no. 36.

characteristics of the areas occupied by the respective associations, it will first be necessary to devise methods, and frequently instruments also, by which the climatic conditions of any given area may be so integrated as to bring out their relations to the processes of growth and reproduction in organisms. In the beginning, such methods will usually need to deal with single conditions or factors as they influence physiological phenomena, but biological science must eventually appreciate that single conditions, or any group of conditions comprising less than all the effective ones, cannot be considered as determining natural processes. Complexes of environmental factors must needs be analyzed into simpler ones, for purposes of study, but after knowledge of the effectiveness of each has been experimentally obtained (through maintaining all conditions other than the one in question not only constant but at a known and stated value or intensity), they must then be recombined and their effects integrated before real knowledge may be available.

If a plant thrives in a given locality, so as to form a part of the flora of that locality, it is obvious that there have not occurred here, since the arrival of its ancestors, any environmental conditions incompatible with its existence. In this we merely make the biological observation that the organism is and has been *adapted*[2] to the environment in which we find it, and that the environment is and has been *adapted* to the organism. Thus, when the range or geographical extent of an organism or association has been determined, it is clear that the area or areas so circumscribed have been characterized for some time in the immediate past by conditions none of which have been adverse enough to annihilate the forms dealt with. Outside of these areas the conditions have not been such as to bring about the permanently successful entrance of these forms, up to the present time. It is of course clear that entrance may have been accomplished here, but if this has been the case each such entrance must have been followed by the occurrence of annihilating conditions.

[2] On a somewhat matter-of-fact view of biological adaptation, see the following paper: LIVINGSTON, B. E., Adaptation in the living and non-living. Amer. Nat. 47:72–82. 1913. See also HENDERSON, L. J., The fitness of the environment. New York. 1913.

Furthermore, the internal conditions (or the nature) of an organism being duly considered, the success attained by it in any locality is an index of the extent to which the environmental conditions of that place have been favorable to successful growth, both vegetative and reproductive. Thus it frequently becomes apparent that the conditions of one locality have been more or less favorable to the success of a given form than have those of another locality.

The difficulty, however, which ecological science has not yet been able to surmount lies in the extreme complexity of the system of conditions which affect the success of organisms. The numerous component factors of an environmental complex fall into categories of *water*, *non-aqueous materials*, *heat*, *light*, and *mechanical conditions*. It is obvious that the limiting condition that has prevented the occurrence of a certain plant, for example, in a given area, may belong to any one of the foregoing categories; mechanical conditions may have failed to bring the seed hither, moisture conditions, or other conditions of material supply or removal, may have annihilated the plant after it was really introduced, or annihilation may have followed from adverse temperature or light conditions, etc.

The distributional problem is made still more complicated and difficult by the perfectly clear but seldom emphasized proposition, that each separate or component condition of an environmental complex is a variable in at least two dimensions, as it were; each such condition must always be considered with regard to its *intensity* and also with regard to its *duration*. To illustrate by means of a water factor, a desiccated soil may cause the death of a given seed, but this result would probably not be accomplished if the soil were dry for only a day or a month; the condition of dry substratum must be maintained for a certain minimum period if it is to be effective as a limiting condition. Some less well defined environmental factors have to be considered in regard to a third dimension which may vary, namely, *quality*. Light, for example, may reach chlorophyll tissue in seemingly sufficient intensity and during an apparently sufficient time period to produce a requisite amount of carbohydrate, but this may fail to happen because the radiant energy is of too short or too long wave-length. Here quality is as important as is either intensity or duration.

Finally, the difficulties of distributional, as of other physiological problems, are greatly aggravated by the fact that each organism is always in process of internal alteration, passing thus through various more or less well defined and conveniently separable phases of development. Thus, a certain quality, intensity, and duration of the light condition may be wholly without sensible effect upon an unsoaked seed, while the same dimensions of the same factor may be fatal to the same plant when in a more active developmental phase. In the study of external conditions it is thus useless to attempt to establish relations between these and organisms, unless adequate consideration is given to internal conditions or developmental phases of the latter. Quantitative ecology must not only try to find out to what environmental conditions its organisms are subjected, and to what degree and for how long these conditions are present, but it must also determine during what developmental phases of the organisms the conditions are effective. It is this consideration which makes it quite impossible to establish ecological relations without adequate knowledge of the physiological nature, at different developmental stages, of the forms dealt with.

Leaving temporarily out of account those mechanical conditions which may, in the past, have acted to transport plants from one geographical area to another, we are aware that the environmental conditions which control growth and reproduction, after the introduction of an organism into a given region, are nearly always naturally in a state of flux. Day and night changes and the march of the seasons, together with more markedly irregular fluctuations in wind, precipitation, evaporation, etc., all produce their effects upon both living things and non-living ones, but these effects are usually much more pronounced in the case of organisms than in that of inanimate objects. As has been previously emphasized by one of the writers,[3] an organism furnishes, at any instant, a summation of the effects of all the processes which have gone on in the body during its previous developmental history. One of our greatest difficulties, however, lies in the fact that we are totally unable to differentiate this integrated record, but we may nevertheless be

[3] LIVINGSTON, B. E., Climatic areas of the United States as related to plant growth. Proc. Amer. Phil. Soc. **52**: 257–275. 1913.

sure that each of its component terms involves at least a quality, intensity, and duration of some environmental factor. It is thus seen that what is most needed for etiological studies of the geographic distribution of organisms, as well as for all other studies which deal with the conditioning or causation of life processes, is comparative measurements of these processes, or of groups of them, and corresponding measurements of the conditioning environmental factors. To accomplish such measurements and thus to institute the requisite comparisons is now practically impossible in most cases; methods need first to be devised and then to be applied, and the world does not yet offer satisfactory facilities for either. Measurements which can be carried out in present-day laboratories, while applicable in some cases, especially with forms not influenced by light, are quite inadequate even for making a rational beginning in the quantitative study of environments in general. In planning a campaign for this sort of study it is obvious that the effects produced by any environmental factor cannot be adequately studied unless that factor, as well as all the other effective ones, is under control by the experimenter. A laboratory where such experimentation as is here indicated may be carried out is now feasible, with recent advances made in the physical sciences and in physiology, and the scientific and practical importance of the results to be obtained, especially from the standpoint of agriculture and forestry, may perhaps soon warrant the provision of the needed facilities, somewhere in the world.[4] Until such facilities may have become available, it will be profitable, however, to prepare the way for them by carrying out such quantitative or semi-quantitative comparisons between vital activities and environmental conditions as are at present possible.

The present paper involves some of the results of an attempt to find a rational method for interpreting climatic temperature data for phytogeographic purposes. This sort of study is somewhat simplified, in the case of plants, by the fact that the temperature of

[4] This need was strongly emphasized over two decades ago by ABBE, who also quotes DECANDOLLE to the same effect. See ABBE, C., First report on the relations between climates and crops. U.S. Dept. Agric., Weather Bureau, Bull. 36. p. 23, 1905.

the plant body follows very closely upon that of the surroundings, and that soil temperature and air temperature are, roughly speaking, somewhat closely related. Furthermore, the heat condition of plants, as approximately measured by the temperature of the surrounding air, varies only in respect to intensity and duration; qualitative fluctuations are not met with here. Geographically, the present study deals with the area occupied by the United States.

Direct temperature summation

The effectiveness of temperature conditions to promote plant growth in any locality has been measured by phenologists,[5] by means of the direct summation of the daily mean temperatures, such summation extending through the period of any particular phase of plant development which might be considered; for example, the period extending from the time of germination to that of flowering or of seed-maturation. In these temperature summations a certain minimum temperature is assumed as a starting-point, and the amount added to the summation for each day as the season advances is the number of degrees, above the assumed minimum, which represents the mean temperature for that day. The minimum has sometimes been 0° C., more often a somewhat higher temperature. In the employment of such temperature summations, each station of observation is characterized each year by its summation index, and after a period of years these indices may be averaged to give a measure of the temperature factor in general, for that particular place.

In a way somewhat similar to that followed by workers in phenology, MERRIAM[6] has obtained normal summation indices of temperature for a large number of stations in the United States, and has presented these in the form of a chart showing climatic zones, each characterized by its own range of temperature summa-

[5] In this connection see ABBE, *loc. cit.*

[6] MERRIAM, C. H., Laws of temperature control of the geographic distribution of animals and plants. Nat. Geog. Mag. **6**: 229–238. 1894. The same work was again reported, in still more abbreviated form, in part III of the following paper: MERRIAM, C. H., Life zones and crop zones of the United States. U.S. Dept. Agric., Div. Biol. Survey, Bull. 10. 1898.

tion indices. So far as we know, this is the first chart of its kind to be prepared upon the basis of temperature summation, and the temperature zones of this writer have come into rather general use among American phytogeographers.

A method of direct summation, similar to those employed by phenologists but dealing in a more refined way with the temperature conditions of plant environments, has been described by MACDOUGAL.[7] This author summed the temperatures above the freezing-point of water for the period occupied by certain developmental phases of certain plants; but, instead of adopting as the terms of the summation the daily means or the means of daily maxima and minima, his integration was performed, with a planimeter, upon automatically traced thermograph records. The resulting indices of environmental heat conditions are expressed by MACDOUGAL in terms of "hour-centigrade-degree" units. This method has never been employed in climatological or phytogeographical studies, so far as we are aware. It seems to be the simplest and most promising of all the direct summation methods, but of course requires reliable thermograph tracings. Each year or season is to be treated separately, and the resulting annual indices may be averaged for a period of years, to give a normal index.

Temperature efficiencies

Although such temperature summations as those of the phenologists and of MERRIAM have seemed in many instances to furnish data consistent among themselves and constituting on an empirical basis an apparently reliable criterion for the measurement of the intensity and duration aspects of the temperature factor, yet it must be regarded as highly improbable that any fundamental and general principle regarding the influence of temperature on plant life may be derived from the relations thus brought out. It seemed to us that the apparent value of temperature summations must rest upon some basic principle of physiology not indicated in the summations themselves.

[7] MACDOUGAL, D.T., The temperature of the soil. Jour. N.Y. Bot. Garden 3:125–131. 1902.

Now, as far as temperature influence is concerned, the most fundamental generalization that physiology has yet been able to attain is that which may be termed the principle of temperature coefficients. This is primarily the application of the chemical principle of VAN'T HOFF and ARRHENIUS to vital phenomena. This principle states that, within limits, the velocity of most chemical reactions doubles or somewhat more than doubles for each rise in temperature of 10° C.[8] The principle fails to hold rigidly, even in the somewhat vague form in which it is stated, but it seems to express in an approximate way a fairly general truth in chemical phenomena.

A considerable literature has developed about the application of this chemical principle in physiology. CLAUSEN[9] determined the rate of evolution of carbon dioxide from seedlings and buds at several different temperatures and found that this rate somewhat more than doubled for each rise in temperature of 10°, up to an upper limit of about 40° C. COHEN[10] calculated from measurements of O. HERTWIG[11] that the time consumed by developing frog's eggs, for the completion of certain developmental phases, about doubled for each *fall* in temperature of 10°. Miss MATTHAEI[12] studied the influence of temperature on the evolution of carbon dioxide from leaves in darkness and also on the fixation of this gas by leaves in light, and showed that the VAN'T HOFF–ARRHENIUS principle holds also for these plant processes. A temperature coefficient of the same order of magnitude as is required by this principle was found, for a number of different physiological pro-

[8] For one clear statement of this principle see VAN'T HOFF, J. H., Lectures on theoretical and physical chemistry, translated by R. A. LEHFELDT. London. No date (author's preface dated 1898). Part I. pp. 227 f.

[9] CLAUSEN, H., Beiträge zur Kenntnis der Athmung der Gewächse und des pflanzlichen Stoffwechsels. Landw. Jahrb. **19**:893–930. 1890.

[10] COHEN, E., Lectures on physical chemistry for physicians and biologists. Translated by MARTIN H. FISHER. New York. 1902.

[11] HERTWIG, O., Über den Einfluss der Temperatur auf die Entwicklung von *Rana fusca* und *Rana esculenta*. Arch. f. Mikroscop. Anat. und Entwicklungsgesch. **51**:319–381. 1898.

[12] MATTHAEI, GABRIELLE L. C., Experimental researches on vegetable assimilation and respiration. III. On the effect of temperature on carbon dioxide assimilation. Phil. Trans. Roy. Soc. London B **197**:47–105. 1904.

cesses in animals, by LOEB[13] and his co-workers, and SNYDER[14] has emphasized the value of non-chemical temperature coefficients in the study of physiological velocities. An excellent statement of this whole problem, especially with regard to plants, is included in BLACKMAN'S Dublin presidential address,[15] where he discusses also the determination of the effect of temperature on the rate of division of the flagellate *Chilomonas paramoecium*, as carried out by MALTAUX and MASSART,[16] and points out that the temperature coefficient here really dealt with has a magnitude of about 2.4. BLACKMAN'S concluding sentences in this address are worthy of quotation here, for their general bearing on the nature of the question with which we are dealing:

> To me it seems impossible to avoid regarding the fundamental processes of anabolism, katabolism, and growth as slow chemical reactions catalytically accelerated by protoplasm and inevitably accelerated by temperature. This soon follows if we once admit that the atoms and molecules concerned possess the same essential properties during their brief sojourn in the living nexus as they do before and after.

In much of the work that has been published on vital temperature coefficients, relatively simple physiological processes have been considered, and it seems allowable to conclude, at least tentatively, that most of the elementary chemical processes of living things go on according to the principle of VAN'T HOFF and

[13] An apparently complete list of citations for the contributions bearing upon this general subject, including those here referred to, up to November 1908, is given in the following personally polemical article: LOEB, J., ROBERTSON, T. B., MAXWELL, S. S., and BURNETT, T. C., On the encouragement of Mr. CHARLES D. SNYDER. Science N.S. **28**:645–648. 1908. This paper is to be read in connection with SNYDER'S calmer reply: SNYDER, C. D., A reply to the communication of Messrs. LOEB, MAXWELL, BURNETT, and ROBERTSON. Science N.S. **28**:795–797. 1908.

[14] SNYDER, C. D., Der Temperaturkoefficient der Geschwindigkeit der Nervenleitung. Arch. Anat. und Physiol., Physiol. Abt. Jahrg. 1907. 113–145.

———, A comparative study of the temperature coefficients of the velocities of various physiological activities. Amer. Jour. Physiol. **22**:209–334. 1908.

[15] BLACKMAN, F. F., The metabolism of the plant considered as a catalytic reaction. Presidential Address, Botanical Section, British Association, Dublin meeting, 1908. Science N.S. **28**:628–636. 1908.

[16] MALTAUX, MARIA, and MASSART, JEAN, Sur les excitans de la division cellulaire. Ann. Soc. Roy. Sci. Méd. et Nat. Bruxelles **15**:1–53. 1906; Recueil de l'Inst. Bot. Bruxelles **4**:369–421. 1906.

ARRHENIUS, and that such processes possess temperature coefficients, within the ordinary limits of environmental temperatures, of an order of magnitude of from about 2.0 to about 2.5. This may be regarded as a fundamental principle in physiology.

When, however, many of these elementary or component processes are combined into a complex resultant, such as we have in physiological growth, for example, it is not immediately clear on a priori grounds that temperature coefficients of this same order of magnitude must obtain. RUSSELL[17] states rather authoritatively that "the effect of temperature on the *rate of growth* of a plant is in nowise like its effect in accelerating chemical change," and cites the work of BIALOBLOCKI[18] in support of this view. The last named writer studied the influence of temperature upon the rate of growth of barley, and his results appear to show (see RUSSELL'S graph, p. 21) that the value of the temperature coefficient in this case alters markedly with the temperature itself. Considering, however, the fact that these results of BIALOBLOCKI appear to differ very markedly from those of the later workers who have dealt with the question, we are inclined not to give them such conclusive weight as does RUSSELL. In considering the matter before us, it is to be remembered that the principle of VAN'T HOFF and ARRHENIUS has never been supposed to hold, even for simple chemical reactions, excepting *between certain limits*, and that these limits should not be expected to be the same for all processes. Furthermore, as has been emphasized by BLACKMAN,[19] RUSSELL (*loc. cit.* pp. 20 f.), MITSCHERLICH,[20] and others, the full possible effect of a rise in temperature is frequently precluded by the failure of some other environmental condition correspondingly to alter. To illustrate, we may suppose (as BLACKMAN, *loc. cit.* 1908, suggests) that the

[17] RUSSELL, E. J., Soil conditions and plant growth. London. 1912.

[18] BIALOBLOCKI, J., Über den Einfluss der Boden wärme auf die Entwicklung einiger Culturpflanzen. Landw. Versuchsstat. **13**:424–472. 1870.

[19] *Loc. cit.;* also BLACKMAN, F. F., Optima and limiting factors. Ann. Bot. **19**:283–295. 1905.

[20] MITSCHERLICH, E. A., Das Gesetz des Minimums und das Gesetz des abnehmenden Bodenertrages. Landw. Jahrb. **38**:537–552. 1909.

———, Über das Gesetz des Minimums und die sich aus diesem ergebenden Schlussfolgerungen. Landw. Versuchsstat. **75**:231–263. 1911.

velocity of a given chemical process doubles with each rise of 10° in temperature, but that the process is retarded by the accumulation of the products of the reaction. In such a case it is obvious that, with increasing temperature, a point might sooner or later be reached at which the removal of these products might not proceed rapidly enough to allow the full temperature effect to become manifest. Thus, the rate of removal of the products must be adequately increased with the rise in temperature; otherwise the effect of this rise becomes masked by the effect of another variable, namely the mass action of the products. From these considerations it does not seem surprising that complex vital processes such as growth may frequently fail, under natural conditions, to exhibit the usual chemical temperature coefficient. In some of these cases, proper alterations in other environmental factors might disclose the otherwise obscured coefficient; in other cases the limitations might lie in the nature of the protoplasmic mixture, and the obscuring of the coefficient might persist in spite of any attempt at external adjustment.

The most satisfactory study on the influence of temperature upon growth rates in plants, so far as our knowledge goes, is that of PRICE,[21] who determined temperature coefficients for the opening of flower buds of the plum, peach, apple, and other fruits, and found the VAN'T HOFF–ARRHENIUS principle generally to hold. Beginning with resting buds, the time period required for blooming is reduced about one-half for each rise in temperature of 10° C. The same author figures maize seedlings which suggest that the rate of growth in length of shoot about doubles for each rise of 10°.

The present aspect of the entire question leads us to the conclusion that there are many cases in which growth rates and other complex processes in plants and animals exhibit temperature coefficients of about 2.0, and that, in other cases, this same coefficient may probably be operative, but may be obscured by the limiting effect of some other environmental or internal condition. It must also be supposed that temperature coefficients of other orders of magnitude may be encountered, not only for complex life

[21] PRICE, H. L., The application of meteorological data in the study of physiological constants. Ann. Rep. Virginia Agric. Exp. Sta. 1909–1910.

processes, but also for some of the elementary ones. The elementary processes of growth itself (that is, the *immediate* phenomena which condition growth, the ones first met with in a rational attempt to analyze the complex process) are all or nearly all physical in nature, and not to be regarded as chemical. They include such physical changes as coagulation, precipitation, alterations in elasticity, swelling by imbibition and osmotic action, and many others. It thus becomes apparent that the reason why the chemical temperature coefficient appears to be manifest in growth phenomena cannot be that these phenomena are primarily and immediately chemical in their nature, but that, physical though they are, they depend in turn upon other internal changes that are unquestionably chemical. Thus, for a single example, the precipitation or coagulation of colloid material met with in the formation of cell walls in plants must logically be dependent upon the continuous presence of the precipitating substances in the peripheral layer of the protoplasm of each growing cell, and within a certain range of concentration, and this continuous presence indicates chemical processes which must be effective not very far back (in the chain of causally connected phenomena) from the precipitation itself. Under such circumstances it might be expected that a physical complex such as growth would frequently exhibit a chemical temperature coefficient.

The fundamental physical changes which make up growth have not yet been studied sufficiently to permit the making of any estimate regarding the orders of magnitude of their temperature coefficients; nevertheless, we are certain that some of these coefficients possess values widely different from that postulated by the VAN'T HOFF–ARRHENIUS principle. Thus, for example, the temperature coefficient of osmotic pressure, within the range encountered in living cells, approximates the familiar quantity 0.003665, as usually employed, for each single degree above the zero point of the Centigrade scale, the pressure at 0° being taken as a basis. If the pressure at 0° be considered as unity, the pressures at 4°, 14°, 24°, and 34° become 1.01466, 1.05131, 1.08796, and 1.12461, respectively, and for each 10° rise in temperature the pressure is increased by only about 0.04.

On the other hand, within the temperature range with which physiology deals, some physical phenomena exhibit temperature coefficients somewhat closely approximating the order of magnitude called for by many chemical reactions. To illustrate, the vapor tension of water at 4°[22] is 6.097 mm. of mercury, and the tensions at 14°, 24°, and 34° are 11.908 mm., 22.184 mm., and 39.565 mm., respectively. Here the three temperature coefficients corresponding to these three rises of 10° in temperature are 1.95, 1.86, and 1.78, respectively. The vapor tension of water must be accounted an important condition for all transpiring plants; this pressure may be regarded as the driving force of evaporation, thus constituting the fundamental energy condition of the phenomenon of transpiration.

Application of temperature coefficients to climatology

If the processes of growth and development do really exhibit temperature coefficients, it is plain that the study of environmental integrations should deal with these rather than with temperatures directly. It is also plain that if direct temperature summations do, in certain cases, furnish adequate criteria for evaluating the effectiveness of temperature conditions, then this state of affairs must be true only within certain limits, and the experimental study of temperature coefficients furnishes the only adequate means for locating these limits and establishing the direct summations upon a rational basis. It seems worth while, therefore, to make a first attempt in the direction of the application of velocity coefficients to the study of effective temperature conditions as these characterize climatic and vegetational areas. Such an attempt, of course, must be very unsatisfactory from an idealistic point of view; nevertheless, it should serve to emphasize the need of quantitative studies in this connection and should also be of value in showing what sort of climatic and distributional observations are most likely to be of value as ecology becomes more exact.

For the present study we have tentatively assumed that the temperature coefficient of growth and development has a value of 2.0 for each rise of 10° C., a value which somewhat closely approxi-

[22] BIEDERMAN, R., Chemicker Kalendar. 1903. Bd. 2. Berlin. 1903. pp. 84, 85.

mates those which have so far resulted from most physiological studies of temperature relations. It seems that this value is more likely to be too low than too high for ranges of temperature commonly met with in nature, but the present status of the problem does not warrant any attempt at a closer approximation. Indeed, it seems almost certain that the magnitude of the temperature coefficient will be found to vary, not only with different plant forms and with different stages of development of the same form, but also with the values of the temperatures considered. It is readily conceivable that the relation which we are seeking may be determined satisfactorily only by the use of a temperature coefficient which is itself a variable, changing in value with the progress of the organism through its life cycle and with the annual march of the seasons, as well as with variations in the temperature itself. The time is not yet ripe, however, for even an a priori discussion of this matter.

Having tentatively established the temperature coefficient which is to be taken as a measure of the effectiveness of temperature in advancing growth (the intensity factor), we must make a similar assumption in case of the duration factor. For what period of time should we apply our assumed temperature coefficient? This question is precisely the same as the one met with in connection with direct temperature summations, and its answer, as in that case, must involve the relation of time to the developmental stages in the organisms concerned. Since it is here desired to deal with the whole matter in the broadest and most general way, it is requisite to fix upon a time period, which will, as nearly as possible, approximate the period of active growth in the majority of higher plants. As one of the authors[23] has emphasized, the controlling climatic conditions are primarily effective for most plants only during the season of active growth. This growing season may be approximated, for phytogeographical purposes, as the average or normal length of the frostless season, the number of days which intervene between the average date of the last killing frost in spring and the first in autumn. This has been adopted as the time factor in the present study.

[23] Proc. Amer. Phil. Soc. 1913; as already cited.

Since the individual data from which was derived DAY's chart[24] of the average length of the frostless season in the United States have not been published as such, the average lengths of the frostless season for the various stations in the United States with which we have been concerned have been taken from the 106 climatic summaries by sections,[25] published by the Weather Bureau.

Not only is it necessary to fix upon the length of time during which temperature integration is to be made, it is also requisite, for each station, to establish the month and day with which the summation is to begin, and likewise that with which it is to terminate. These dates must of course be chosen with reference to the beginning and ending of the period of active growth. The first is here taken as the date *next following* the average date of the last frost in spring, and the second as the average date of the first frost in autumn. If the dates for the beginning and end of the assumed growth period were determined from daily mean temperatures (as in case this period were taken as beginning with the first day in the year having a daily mean of 40° F. or above, and ending with the last day having this temperature), then they should bear a definite relation to the real first and last dates of the active period. Such methods have been frequently used in phenology. By our method, the beginning and end of the average period of active growth are determined from frost data rather than from mean daily temperatures. The two methods would probably prove equally satisfactory, with no great discrepancy in most cases.

The geographical distribution of plant associations and of species involves the effectiveness of climatic features throughout many years, and a knowledge of these features for any single year is of but little value in the present connection. This consideration involves still another sort of climatic integration that has not yet been mentioned here; namely, the averaging of the effective conditions for long periods of time. This operation has been implied, however, in the preceding treatment of the average length

[24] DAY, P. C., Frost data of the United States, etc. U.S. Dept. Agric., Weather Bureau, Bull. V. 1911.

[25] Summary of the climatological data of the United States, by sections. U.S. Dept. Agric., Weather Bureau. No date. These pamphlets appear to have been prepared about 1909–1910. The data generally extend through 1908 or 1909.

of the frostless season. For the intensity factor of temperature effectiveness it is necessary to employ as data, not the temperature of any single instant, nor the mean temperature of any single day, but what has been termed the *normal mean* temperature for each day of the frostless season. Fortunately, these data have been calculated by BIGELOW and have been made available through publication by the U.S. Weather Bureau.[26] These have been here employed.

The plan of this study is: (1) to sum the normal daily mean temperatures of each station considered, for the period of the average frostless season; (2) to sum the temperature efficiencies corresponding, respectively, to the normal daily means and to the adopted coefficient for 10° of variation; (3) to plot both sets of temperature indices so obtained in the form of charts; and (4) to compare the form and location of the climatic areas or zones thus exhibited.

The temperature indices

As in the case of direct temperature summations, so in that of the summation of temperature efficiencies, it is necessary to establish a temperature which may be taken as a starting-point. This should approximate the temperature at which general plant growth is evident and should be chosen according to the same criteria as are employed by phenology in similar cases. For both series of summations we have taken the rate of growth and development as unity with a daily mean temperature of 40° F. (4.4° C.). Normal daily means below 40° F. do not occur in BIGELOW's tables. If they did occur, growth on such dates would be taken as nil, on the basis of our assumptions.

For each of the direct summations, the normal daily mean *minus* 39, for the date next following the average date of the last frost in spring, is taken as the first term. To this are added the normal daily means, each decreased by 39, for all dates up to and including the average date of the last frost in autumn. Practically, the summation of the unmodified normal daily means was first made

[26] BIGELOW, F. H., The daily normal temperature and daily normal precipitation of the United States. U.S. Dept. Agric., Weather Bureau, Bull. R. 1908.

for the period and then a quantity equal to 39 times the number of days in the average frostless season was substracted from the sum.

For the summations of temperature efficiencies, the normal daily efficiencies corresponding, respectively, to the normal daily means of BIGELOW'S tables have simply been added for the same days as in the direct summations, thus giving what may be termed a tentative index of temperature efficiency for growth during the normal frostless season. We shall term this the *efficiency index* and the direct summation will be called the *direct index*. It is these two indices and the charts formed from them that are to be compared.

To obtain the daily temperature efficiencies corresponding to the various normal daily temperature means as the latter are given by BIGELOW, it is necessary merely to deduce them from our basic assumption, namely, that the growth rate is unity at 40° F., and that it doubles for each rise of 10° C. (18° F.) above this. We shall employ the Fahrenheit scale, not because it is in any way as satisfactory as the Centigrade, but because temperature observations in the United States and the published data deduced therefrom have the antiquated form.

If t be taken as the normal daily mean temperature on the Fahrenheit scale, and if u be the corresponding temperature efficiency for growth, according to our assumption, then

$$u = 2^{\frac{t-40}{18}} .$$

It is clear that this equation fulfils the assumed conditions, that the efficiency doubles with each rise of 18° F., for, if t is 40° F., then u is unity; if t is 58° F., then u is 2; if t is 76° F., then u is 4; and so on. It becomes necessary, therefore, merely to interpolate between the already known values the various values of u corresponding to the actual values of t which are to be dealt with. The equation just given may as well be written

$$\log u = \frac{\log 2}{18}(t-40) ,$$

from which the requisite values of u may readily be obtained. Another way of stating the above relation is this: The tempera-

ture efficiency (u) for any Fahrenheit temperature (t) is the eighteenth root of 2 effected with an exponent equal to the given temperature *minus* 40. From this the values of u may be directly calculated. Only one cycle of eighteen quantities, however, needs to be so determined in any case, for the coefficients of the second cycle are double the corresponding ones of the first, etc.

The following table presents the approximate values, derived as above, for the efficiencies corresponding, respectively, to the temperatures (in whole degrees) from 40° to 99° F.

APPROXIMATE EFFICIENCY INDICES FOR TEMPERATURES, IN WHOLE DEGREES, FROM 40° TO 99° F., ASSUMING THE EFFICIENCY TO BE UNITY AT 40° AND TO DOUBLE WITH EACH RISE IN TEMPERATURE OF 18 DEGREES

Temperature, degrees F. (t)	Efficiency (u)	Temperature, degrees F. (t)	Efficiency (u)	Temperature, degrees F. (t)	Efficiency (u)
40	1.0000	60	2.1603	80	4.6662
41	1.0393	61	2.2451	81	4.8490
42	1.0802	62	2.3331	82	5.0396
43	1.1226	63	2.4245	83	5.2384
44	1.1666	64	2.5198	84	5.4424
45	1.2123	65	2.6192	85	5.6568
46	1.2599	66	2.7212	86	5.8782
47	1.3096	67	2.8284	87	6.1090
48	1.3606	68	2.9391	88	6.3496
49	1.4142	69	3.0545	89	6.5972
50	1.4696	70	3.1748	90	6.8566
51	1.5273	71	3.2986	91	7.1258
52	1.5874	72	3.4283	92	7.4048
53	1.6493	73	3.5629	93	7.6960
54	1.7142	74	3.7024	94	8.0000
55	1.7815	75	3.8480	95	8.3144
56	1.8512	76	4.0000	96	8.6412
57	1.9240	77	4.1572	97	8.9804
58	2.0000	78	4.3206	98	9.3324
59	2.0786	79	4.4902	99	9.6980

Efficiency indices and direct indices for the mean frostless season in the United States

All of the climatological calculations involved in this study have been carried out, and at least once repeated, on a computing machine.[27] The stations employed (179 in number) are those of

[27] The authors wish here to acknowledge with thanks that they have had the assistance, at various points in this work, of Mrs. EDITH B. SHREVE, Mr. H. E. PULLING, and Mr. J. W. SHIVE. It is also a pleasure to state that the study was made possible by the Department of Botanical Research of the Carnegie Institution.

BIGELOW's paper already cited, with a few omissions on account of the lack of corresponding frost data. Each series of summation indices was placed upon a large map of the United States, and the map was then divided into areas by isoclimatic lines, in the usual way. Thus were obtained two charts, one showing the geographic range of the efficiency indices and the other the corresponding range of the direct ones.

It was at once observed that the relations of the different areas to one another are surprisingly similar in the two charts, so that one chart appears about as valuable for bringing out the temperature characteristics of phytogeographic areas as does the other. A detailed study of the two charts, however, made it clear that they differ, as regards the relative form and relative numerical characteristics of their respective zones, in many particulars. The two charts are here presented as figs. 1 and 2. The numerical efficiency data from which these charts were derived (with the aid, at certain points, of probabilities based upon topographic contour lines represented on the original maps[28]) are each placed near the position of the corresponding station, the latter represented by a small circle (for the names of the stations employed, see BIGELOW, *loc. cit.*). To compare the two series of indices, the ratio of each direct index to the corresponding efficiency index was obtained, thus giving a ratio for each station. These ratios have been placed upon a map in a manner quite similar to that used in charting the indices themselves, and the resulting chart, with its isoclimatic lines, is presented as fig. 3.

The interpretation of our charts as regards plant distribution will not be taken up here. They are to be studied, of course, in connection with DAY's chart of the average length of the frostless season, with the charts given by B. E. LIVINGSTON, and with any vegetation map of the United States which it is desired to interpret along these lines.

As has been mentioned, the charts of figs. 1 and 2 show a marked similarity in the form and position of the isoclimatic lines which are represented. Of course it is at once to be observed that the direct summation indices are uniformly much larger than the

[28] U.S. Geol. Survey contour map of the United States, 18×28 in.

4000
6000
8000
10000
8000
8000
10000
12000
14000
SUMMATIONS

FIG. 1

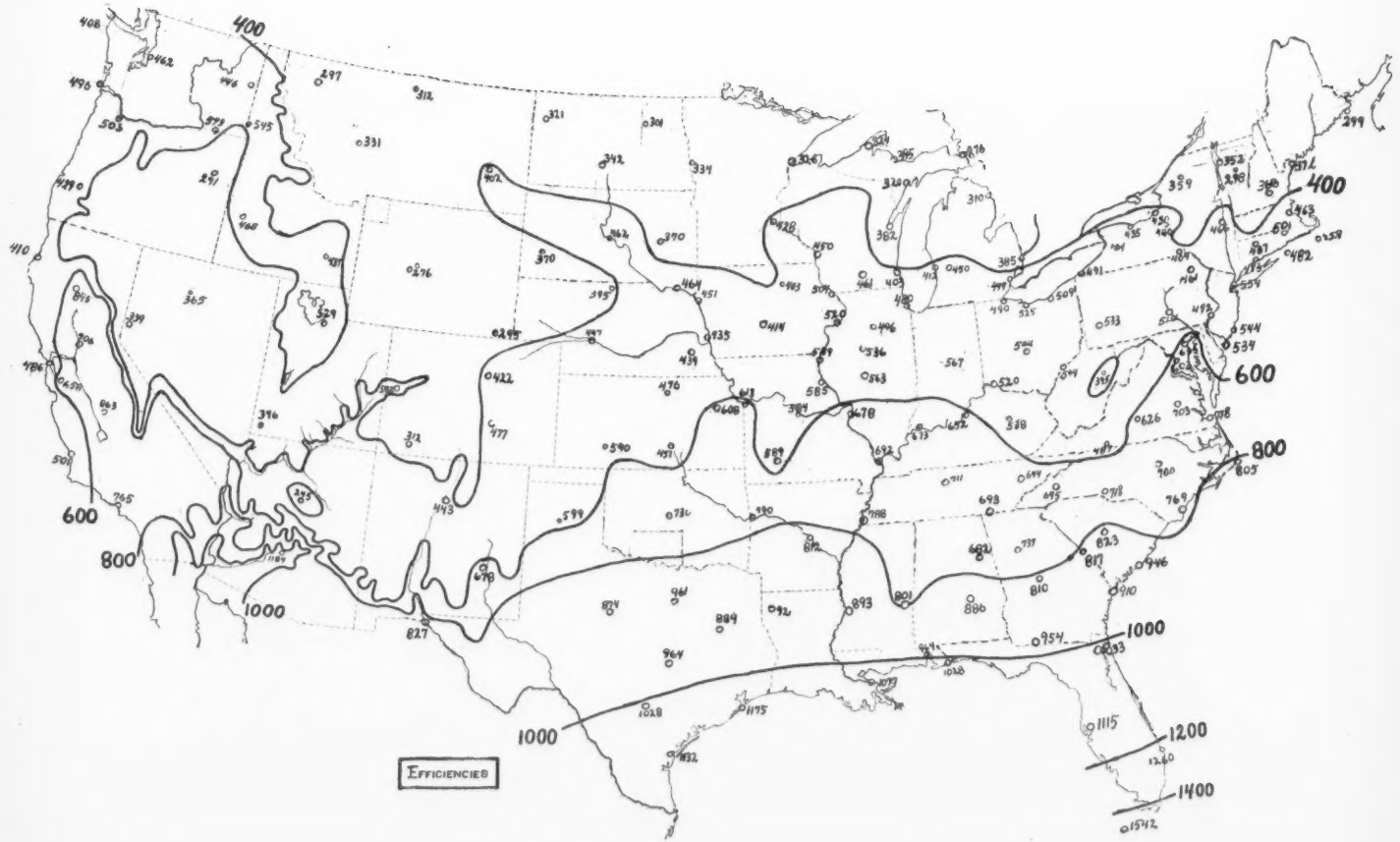

FIG. 2

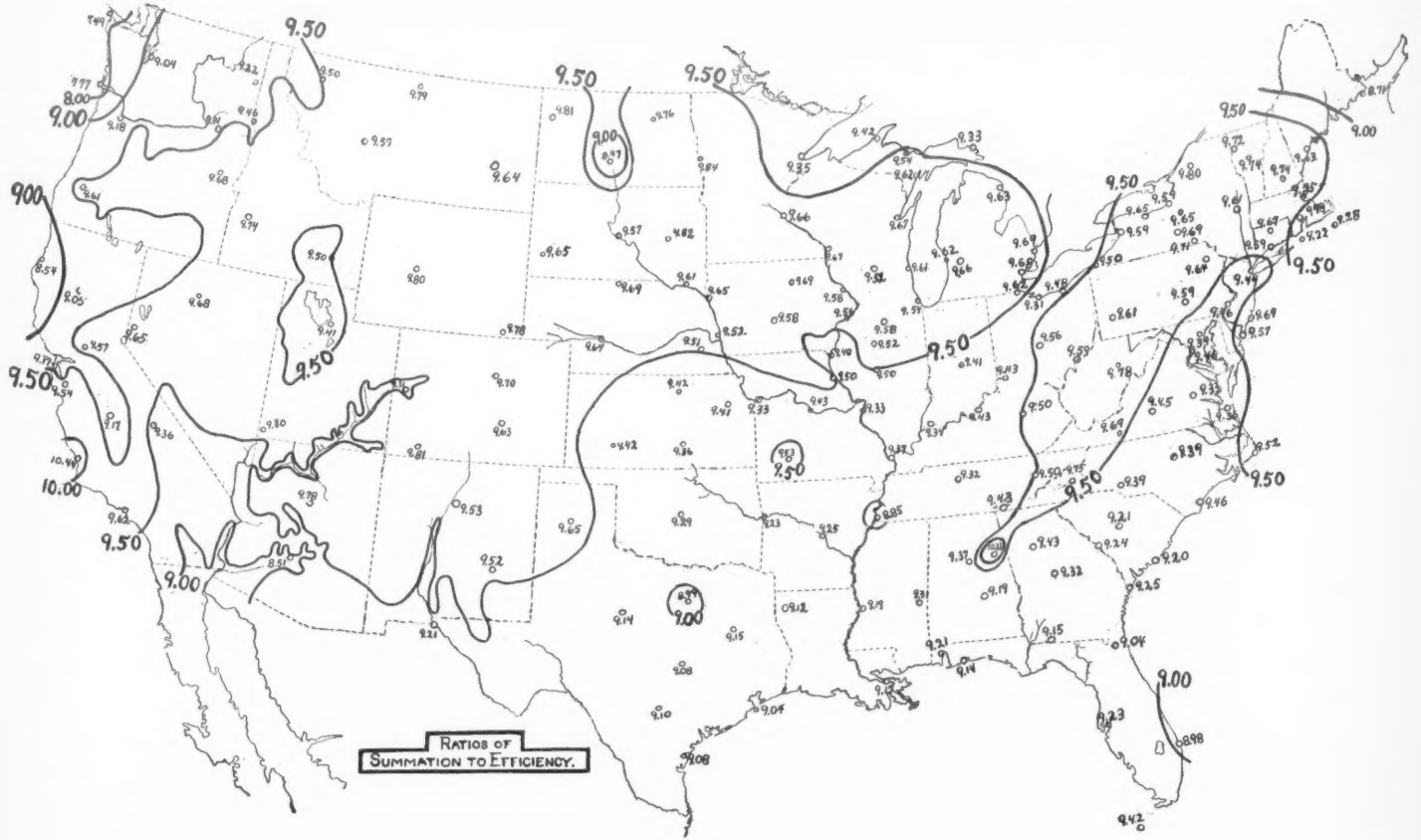

FIG. 3

corresponding ones of the other series, and simple inspection of the two charts seems to indicate that the former indices are rather uniformly about ten times as great as the latter. No ratio between these two indices really exists which is common to all our stations, but what we wish first to emphasize is that the two charts are outstandingly and even surprisingly alike in the general form of their isoclimatic lines. The stations for which data are available are so irrationally distributed over the country (being relatively closely crowded in the eastern part, with low climatic gradients, and widely separated in the west, with high gradients) that an average ratio, or any other statistical function of the ratio series, must be without meaning, but it is clear from the ratio chart (fig. 3) that ratios between 9.00 and 10.00 characterize almost the entire area of the United States. In other words, for the great majority of stations the magnitude of the ratio in question does not depart more than 5 per cent from the value 9.50. Considering that all our original data must be regarded as only roughly approximate, this appears to indicate a very good agreement between the results of the two methods. We may state, therefore, that *for most of the area of the United States*, the two methods here employed for estimating temperature effectiveness for plant growth give results which agree within the limits of a plus or minus variation no greater than 5 per cent. It will be noted that this statement practically involves the placing of the phenological method of direct summations upon a much more satisfactory basis than this method has heretofore possessed; it now appears that the direct summation method gives the same *general* form of chart as does the other method of temperature integration, and this empirical treatment really ascribes to the former method some degree of the theoretical foundation upon which the latter rests.

The similarity between our two summation charts, however, is only approximate and superficial. If it held rigidly, either of the two charts would suffice for both, and any efficiency index might be deduced from the corresponding direct index, merely by dividing the latter by the proper constant. The efficiency indices are not uniformly ten times the summation indices, nor is there any ratio other than ten which may be assumed with the aim of attaining

greater uniformity of detail in the two charts. The numerical data indicate, furthermore, that it would be quite impossible to make one chart more like the other by choosing other values through which to pass the isoclimatic lines.

The most striking difference between these charts (figs. 1 and 2) is seen in the basin and Pacific regions. Nowhere on the Pacific coast does the efficiency index fall below 400, while the northern half of this coast characteristically exhibits direct indices below 4000, Tatoosh Island, Washington, having a direct index as low as 3054. Thus it has been impossible to draw the lines on the chart of direct summations so as to bring the northern area with indices above 4000 (from Great Salt Lake to the Columbia River) into conjunction with the southern area having the same sort of indices (California, Arizona, etc.). On the efficiency chart these two areas become joined, however. Other less striking quantitative differences are clearly enough indicated, and this sort of inspection establishes the fact that the ratio of the direct summation index to that of efficiency can by no means be regarded as constant for the whole country. It is of course to be remembered that the hypsometric map has been called into requisition in the placing of our isoclimatic lines, the stations for which data are available being far too few and too far apart to give the detailed information which such charts require. Nevertheless, it seems perfectly clear that while the isoclimatic lines may really have other positions than the ones here assigned them (it is safe to suppose that almost every centimeter of these lines would be displaced to some extent if more data were at hand), yet the discrepancies between the two charts are not primarily to be related either to lack of data or to careless or inefficient interpretation of the information at hand.

Our arithmetical treatment of this question of the value of the ratio of the direct index to the index of efficiency brings out the fact that this ratio varies, for the stations employed, from 7.49 (Tatoosh Island, Washington) to 10.44 (San Luis Obispo, California) or 10.33 (Anniston, Alabama). As has been mentioned, the values of these ratios are presented in fig. 3, where lines are shown for the ratio values 8.00, 9.00, 9.50, and 10.00. This chart brings out the geographic distribution of these various values.

What may be the meaning of this new kind of climatic chart, as regards vegetational distribution, plant activity, or any other phenomena influenced by climatic conditions, cannot yet be surmised, but the chart does indicate a very important truth as far as climatology and climatological methods are concerned. If we look upon the normal daily mean temperature as in some way involving a criterion for the approximate evaluation of the naturally effective heat supply, it is shown that the summation of these normals for the period of the frostless season does not give, excepting in a very superficial way, the same chart for the United States as does the corresponding summation of temperature efficiencies following the assumptions here made.

It may be said that the direct index is a measure of one dimension of the temperature factor of a climate, while the efficiency index as here employed measures another dimension. Which of the two dimensions more nearly approximates the measure of the temperature effectiveness of a climate, as far as plant growth is concerned, will no doubt remain for a long time undetermined. The present independent status of the direct summation method for the treatment of temperature data rests upon phenological observations in the open, while the status of the other method of treatment (employing temperature efficiencies instead of the daily mean temperatures themselves) is founded upon deductions from the chemical velocity coefficient of VAN'T HOFF and ARRHENIUS, upon physiological experimentation under more or less controlled conditions, and upon the fact that all physiological processes are chemical in their nature or else depend upon other processes which are chemical. It must be admitted, on physiological grounds, that some sort of efficiency summation seems likely to prove more truthful and more valuable in vegetational-climatic studies than the direct summation of temperatures. The latter method of treatment has no a priori or logical basis (although, as has been seen, it is not altogether without pragmatic or empirical points in its favor), and appears, superficially at least, to be quite arbitrary in its theoretical conception.

The details of the distribution of our various ratio values deserve attention, for they bring out quite unequivocally, not only that

these values do indeed vary, but also that their variations are in accordance with the geographical positions of the stations concerned. It is clear from fig. 3 that the portions of the United States characterized by ratios below 9.00 lie mainly near the margins of the country. The lowest ratios of our series occur in western Washington. Other areas with ratio values below 9.00 are indicated for northwestern California, southeastern California and southwestern Arizona, southeastern Florida, northeastern Maine, and north-central North Dakota. It thus appears that a line representing a ratio of 9.00 may be passed, according to the indications of fig. 3, around the area of the United States, entering within its boundaries only sufficiently to include the areas just mentioned.

On the original chart, from which fig. 3 is taken, were drawn lines representing the ratio values by tenths, from 9.0 to 10.0. From this chart (as of course also from the numerical data given in fig. 3) it is evident that the ratio values with which we are dealing are consistently distributed, with few or no exceptions. An area of high ratios occurs in the Appalachian Mountains, having the highest value at Anniston, Alabama (10.33). Another similar area occupies the Rocky Mountains and appears to extend northward to the Canadian boundary, with maximum values of 9.81 (Williston, North Dakota and Durango, Colorado). A small area of high values lies about Moorehead, Minnesota (9.84), and Huron, South Dakota (9.82). A less pronounced but strongly and consistently indicated area occupies the southern peninsula of Michigan and eastern Wisconsin, the maximum here being at Port Huron, Michigan (9.69). Finally, a somewhat questionably indicated area of high ratio values centers about San Luis Obispo, California (10.44). Interior areas of low ratios require no discussion; they are few, and are generally based upon the evidence of single stations.

From the study of this chart it seems clear that the ratios of direct temperature summations, for the normal frostless season, to the corresponding efficiency summations as here derived, must be considered as a measure of some climatic characteristic. Just what this characteristic may depend upon we are not here attempt-

ing to find out; it obviously has to do with the order of magnitude of the normal daily mean temperatures and also with the distribution of these magnitudes throughout the mean frostless season. There seems little doubt that a mathematical treatment involving limits may bring out the nature of those characteristics of the frostless season which are measured by the ratio as employed in this paper.

Conclusions

1. The method of direct temperature summations has proved itself to give, *in a broadly general way* and *for most of the area of the United States*, nearly the same climatic zones as does our method of efficiency summations; for practical purposes and for the present, the former method, till now based solely on phenological observations, seems thus to be placed in closer logical connection with the temperature coefficients of chemical, physical, and physiological processes than has heretofore been the case.

2. The similarity between the results derived by these two methods of temperature integration, however, is only superficial and roughly approximate. The ratios of direct summation to efficiency summation range in magnitude, for the mean frostless season in the United States, from a minimum of 7.49 to a maximum of 10.44.

3. A rational and consistent climatic chart represents the geographical distribution of these ratio values; on such a chart the marginal regions of the country are frequently characterized by low ratios and the two main mountain systems appear to control areas of high values.

4. There seems to be no doubt that the ratio here brought forward quantitatively represents a climatic dimension or characteristic, which appears to be some sort of function of the daily normal temperatures upon which this whole study has been based and of the time distribution of these temperature data within the period of the mean frostless season.

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APOGAMY IN ATAMOSCO

LULA PACE

(WITH PLATES XIII AND XIV)

Atamosco texana Greene (*Zephyranthes texana*) is one of the Amaryllidaceae, and is called amaryllis, atamosco lily, or rain lily. The so-called rain lilies in this region bloom in the summer and autumn for a few days after each rain. This one is not quite so well known here as the white lily, *Cooperia Drummondii*, which is about twice the size and much more abundant in this locality; but 100–200 miles farther west *Atamosco* is the more plentiful.

The first collection of material was made for class use, as the ovules and embryo sac are very large; but very early in the preparation of this material interesting things were noticed. So the material on hand was carried to Bonn and worked over there so far as the stages permitted. I regret exceedingly not being able to complete it at that time under the direction and with the suggestions and criticisms of Professor STRASBURGER. But it gives me great pleasure to acknowledge my indebtedness to him for his kindly interest and stimulating suggestions during the first part of the work.

Material

The material was all collected in one locality, near Waco, Texas; and in this particular place *Atamosco* is quite abundant over two or three acres. But as the flowers are solitary and often precede the leaves, it is not easy to find young stages. I now have plants under cultivation and hope to get these desired stages later.

Two collections have been made, one in 1909 and the other in 1911. The intervening year I was abroad and no collection could be made. The material was fixed in chromacetic acid (0.25 per cent chromic acid and 1 per cent acetic acid). In some cases about 10 drops of 1 per cent osmic acid was added to 50 cc. of the above. Alcohol-acetic (three parts absolute alcohol and one part acetic acid) and alcohol-formalin (two parts of 50 per cent alcohol and one

part of 10 per cent formalin) were also used. The triple stain, safranin, gentian violet, and orange G, and iron hematoxylon were found most satisfactory.

Pollen

The pollen is quite normal in every way in the anthers sectioned (fig. 1). The tube nucleus is usually somewhat amoeboid in shape and occasionally has more than one nucleolus. The generative cell with its nucleus and bit of cytoplasm about it is quite small. In this figure the generative nucleus has the chromosomes segmented. The number is 12 and was counted in several other grains in the same anther. But in the majority of the pollen grains studied the generative nucleus was in the spirem stage (fig. 2). In this same anther a few grains were seen with possibly two generative nuclei; but it is probable they are the sperm nuclei, as they are both in the same cell. A germinating pollen grain from the stigma shows the generative nucleus in mitosis and in advance of the tube nucleus (fig. 3). In fig. 3, *a* this nucleus is shown with greater magnification, and the remainder of this nucleus, which was in the adjacent section, is shown in *b*. The chromosomes show longitudinal splitting and there are 12.

Embryo sac

The mother cell is only slightly larger than the adjacent cells when first distinguishable (fig. 4). The ovule now increases rapidly in size and the mother cell becomes very large. The division of the mother cell has not been seen. Many ovaries with ovules showing large mother cells have been cut, and many that were apparently the same size had mature sacs. The development of the sac must be very rapid, for several ovaries had mature sacs and mother cells apparently occurring together without any definite order. But other ovaries showed all ovules in the same stage of development; one in particular has every ovule with the nuclei of its sac in the third and last division, with all stages of mitosis from well developed spirem to late telophase.

The two-nucleate (fig. 5) and four-nucleate sacs show nothing unusual. The spirem for the next division has the normal appearance. In figs. 6 and 6, *a* the anaphase stage of the two nuclei from

the micropylar end of a four-nucleate sac are shown. The entire figures being found in two adjacent sections, both are drawn separately, as the number of chromosomes is so large that it is difficult to reconstruct the two figures and make one accurate drawing. In one nucleus the spindle is almost parallel with the section. In this spindle at one end 11 chromosomes appear, and the same end in the next section shows 13, giving 24 chromosomes at one end of this spindle. It is not possible to make an accurate count at the other end, but there seems to be about the same number. The other nucleus is almost perpendicular to the section and at one end the 24 chromosomes are unusually distinct. A metaphase from the chalazal end of another four-nucleate sac is shown in fig. 7. It also shows the 24 chromosomes. A similar one might be given from the micropylar end of another sac. A somatic cell taken from the walls of the ovule is given for comparison (fig. 8); it shows 24 chromosomes. Fig. 9 is a telophase of this same division from the micropylar end of the sac. The old spindle of the previous division is still quite distinct, but less so than the spindle of this division. This spindle shows wall beginnings in the one parallel with the sections. Only one end of the other spindle appears in this section, as it is perpendicular to it. But this nucleus, which already has the nuclear membrane developed about it, shows approximately 24 chromosomes.

The 8 nuclei arrange themselves in the usual fashion, egg apparatus, antipodals, and two polars that fuse, each group being very distinct and almost diagrammatically organized. The filiform apparatus is well developed, but not so strikingly as in *Parnassia* (20a). The indentations so noticeable in the *Parnassia* synergids are not often seen at all in *Atamosco* (fig. 10). It was present in a few instances, but was never a deep notch. The only noticeable feature of the sac is the large nuclei containing little other stainable material than the large nucleolus. There are often two nucleoli in the egg and occasionally in the synergid nuclei also. They both stain red in the triple stain, or if stained in the iron hematoxylon, they are apparently alike. The antipodal end of the sac has the usual organization (fig. 11). The three antipodal cells are definitely organized, but are without cell walls. The polars are in contact in

the center of the sac. Fig. 12 shows the egg apparatus after the pollen tube enters. One male nucleus is within the egg near the nucleus, the other is just below it. The primary endosperm nucleus lies just above the antipodals and the fusion of the polars seems to be complete. Fig. 13 shows about the same stage. In this case one male nucleus is still not in contact with the egg, while the other has already fused with the polars, showing only as a bit of very dense nuclear material in the upper part of the primary endosperm nucleus, in which all the nuclei are still evident (fig. 13, *a*). Somewhat earlier stages were found with the polars still quite distinct and the male nucleus some distance away. The adjacent ovule shows a similar condition to that in fig. 13, *a*. Another sac in which the pollen tube has entered is shown in fig. 14. The sperm nucleus is not in contact with the egg nucleus, but the other sperm nucleus has begun fusing with the almost completely fused polars (fig. 14, *a*). Here both sperm nuclei have very dense masses of chromatin, looking like a very thick spirem except for thin places at intervals. These thin places seem to be only very delicate threads which with slight magnification are not easily seen, and the nuclei then have the appearance of having the chromosomes already segmented. In fig. 15 the micropylar end of a sac is given with the male nucleus just in contact with the egg nucleus, but there is no evidence that it is fusing, not even a flattening of either nucleus. The triple fusion is already completed and the spirem is forming for the first division. One part of this nucleus is very much denser than the remainder of it and is probably where the male nucleus entered. The very large nucleolus seems to be budding. In another sac the male nucleus lies directly in front of the egg nucleus, but is not in contact with it, while the primary endosperm nucleus of this sac has completed the first division. Here the wall has formed, but it quickly disappears, for the endosperm contains many nuclei before permanent walls appear. The male nucleus does not always come in contact with the egg nucleus, or if it does, it moves away, as it is not in contact in older stages (figs. 17–23).

About 600 sacs have been seen in which the sperm nucleus is within the egg. In very few instances are they in contact, and these were always the earlier stages. The flowers probably always

wither within 24 hours after opening. Those brought in and pollinated had all done so. These withered flowers show the male nucleus within the egg.

Fig. 16 shows an early prophase in the division of the egg. The spirem develops in the usual way, and is very long. Fig. 17 shows the segmentation completed, with a very pale nucleolus and approximately 24 chromosomes. The male nucleus is at some distance from the egg nucleus and shows no change. Fig. 19 shows a similar stage. In Fig. 20 the nuclear membrane has disappeared. About this stage the male nucleus begins to disintegrate (fig. 18); but sometimes the spindle is forming with the membrane of the male nucleus apparently still intact (fig. 21). A spindle is shown in fig. 22, and here the male nucleus is disorganizing. A late anaphase of the egg has the male nucleus entirely without a membrane (fig. 23). The chromatic material is organized into approximately 12 masses, which seem to be more or less perfectly formed chromosomes, although there are evident signs of disintegration. There is nothing in the egg or in this nucleus itself to suggest the possibility of its being a cell of the embryo. This suggests the possibility of "merogonie."

A somewhat earlier anaphase shows approximately 24 chromosomes at each end of the spindle, and the somewhat elongated male nucleus apparently in contact with the spindle (fig. 24). This sac has four endosperm nuclei, two near the base of the sac and two near the middle. Fig. 25 is that of an undivided egg. The pollen tube has the three nuclei in it. There are about 64 endosperm nuclei in the sac and but little trace of the synergids in the adjacent sections. Other sacs in this ovary have embryos with about 16 cells. It is probably a case of a delayed pollen tube and the primary endosperm nucleus dividing before fusion with the male nucleus, although this is the only instance seen where that seems probable. But as has been said above, most of the material of this stage was pollinated in order to be sure of fertilization. It is also possible for this to be the second pollen tube to enter this sac. But if so, all trace of the other one has disappeared.

The endosperm nuclei often contain 7 or 8 nucleoli, all of which stain a brilliant red in the safranin–gentian-violet combination.

An endosperm tissue 2–4 cells in width, but which does not completely fill the sac, and with many free nuclei still present, is found with the embryo of 30–40 cells. There is such a mass of long curved chromosomes in the endosperm that no satisfactory count could be made from any of my preparations. In several instances one could count 50 and know there were still others. One such nucleus, which was in three adjacent sections, is shown in figs. 26, 26, *a*, and 26, *b*. It seems clearer to show each section separately than to reconstruct the nucleus from the three sections. Here more than 60 chromosomes can be counted in all three sections, but it is certain that there were several cut chromosomes, as some were evidently shorter than others, and in this plant the chromosomes all seem to be approximately the same length. The number would be 60 from the fusion of two polars with 24 each and a sperm nucleus with 12. It is possible that in some cases the polars only enter into the fusion, which would give 48. But the triple fusion seems the common condition in the material examined. This is probably the fourth division of the endosperm of this sac. These divisions are not always exactly simultaneous; for in one instance in the second division one nucleus has completed the mitosis, the new nuclei being already perfect, while the other nucleus was still in the anaphase.

Embryo

The embryo shows nothing unusual in its development. The first division has already been described, and is shown in figs. 20–24. One two-celled embryo was seen with a vertical wall, but in all others it was the usual horizontal wall (fig. 27). This figure shows the pollen tube entering one synergid.

Abnormal sacs

Atamosco also has many sacs in which the arrangement of the nuclei does not follow the usual form. These sacs have the antipodal group in the micropylar end of the sac and egg apparatus at the side. The organization of the two groups of cells is as perfect and as characteristic as if they were in the usual position. About 2000 ovaries have been cut; many were too young to show mature sacs, and of others no record was kept. But in about 300 ovaries

that were mature, there were side eggs in 56 and in these 56 ovaries there were 205 of these abnormal cases. The other sacs in these ovaries had nothing unusual in their nuclear arrangement. In the majority of these abnormal sacs there was nothing unusual except the position of the cells, and only those with cells in unusual positions were included in the above statements.

Fig. 28, however, shows two eggs in the micropylar end of the sac with no synergids. The whole of this sac was not seen, so just what the arrangement of the other cells was could not be determined. Both of these eggs may develop, for a sac was seen with two young embryos, one of about 6 and the other of 10 cells, located exactly as these two egg cells were, and with endosperm of 30–40 nuclei. Two other sacs with embryos similar to this were seen. Occasionally more than two eggs may be organized in a sac (fig. 29). This sac has 5 cells in the micropylar end, all of which look like eggs, and two of which show intermediate characters and may function as synergids. This leaves only one antipodal and two polars which have already fused and lie very near the antipodal. Two eggs and two synergids are sometimes found in the one egg apparatus. Sometimes more than one egg apparatus is organized. One was seen with two at the side of the sac, in addition to the usual micropylar apparatus. Not all of this sac was seen, but it has at least 12 nuclei in it. The egg apparatus in these side positions is usually normal in all other particulars; but in one case in which it is at the side near the antipodal end of the sac, the egg is turned vertically, while the synergids have themselves oriented so as to bring their apices toward the edge of the sac.

What might be called a double sac is shown in fig. 30. There are 15 nuclei present, and it is possible there should be 7 instead of 6 in the micropylar group, making 16 altogether, but in tracing from section to section I could not be quite sure. Fig. 31 is from a sac that is almost normal. It seems to have 4 antipodals, and an egg apparatus of one synergid and one egg some little distance from the micropylar end of the sac. The sperm nucleus is in contact and just behind the egg nucleus. A sperm has probably fused with the polars, as there is a dense portion in this otherwise almost clear nucleus. In many of these sacs the antipodal end contains no

nuclei unless the egg apparatus approaches that region. Fig. 32 is from a sac with 13 nuclei, 7 of which have the organization of the antipodals at the micropylar end of the sac, 4 are in the lower part of the sac near the antipodal region, two synergids and two eggs, while the two polars are the only normal feature of the sac. The pollen tube is entering the egg apparatus.

As was said above, in the large majority of these abnormal sacs there are the usual 8 nuclei, and these have the usual organization, but the groups are not in the usual position. Fig. 33 shows a common arrangement except the antipodals here are not exactly at the micropylar end. The egg apparatus is perfect (fig. 33, *a*), as are the polars and antipodals, each group showing its characteristic differentiation. A four-celled embryo in a similar sac is shown in fig. 34. Here the primary endosperm has not divided. PORSCH (**21**) and those holding the archegonium theory would regard these extra groups as the organization of additional archegonia. If the two groups of cells usually found in an embryo sac are archegonia, the interchange of characteristic organization would not be very remarkable. In the 16-nucleate sac of *Euphorbia procera*, MODILEWSKI (**15**) figures 4 groups of 4 nuclei each. From each of these groups one nucleus moves to the center to form the primary endosperm nucleus, leaving 3 in each of the groups. The micropylar group he calls the egg apparatus, and that one is the only one figured as functioning. But each of the groups at the side of the sac have the appearance of an egg apparatus.

Discussion

The egg apparatus is almost diagrammatic, so the first thing to attract attention was the very small sperm nucleus as compared with the egg nucleus. But as the egg nucleus contains very little stainable material except the nucleolus, while the sperm nucleus is very dense, the real condition was not suspected, for the sperm nucleus is often much smaller than the egg nucleus. LAND (**14**) figures a very small but dense spiral sperm in *Silphium*. NAWASCHIN (**17**) shows a similar one in *Helianthus*. GUIGNARD gives a like condition in *Iris* (**7**), and in some of the Ranunculaceae (**9**) and Solanaceae

(10); and STRASBURGER (27) figures a small more or less coiled sperm for *Urtica dioica*. Less difference in the relative size of the two nuclei appears in *Cypripedium* (19). Other instances might be cited, but these are sufficient to show that a difference in the size of the sex nuclei is not unusual.

Older stages were then cut and a spirem was found in the egg nucleus while the sperm was often not even in contact with it. This was supposed to be a case of the early prophases taking place before the fusion of the sex nuclei. GUIGNARD (8) shows such a case in *Lilium Martagon*, and *Cypripedium* (19) and *Calopogon* (20) both show this condition. BLACKMAN (1), CHAMBERLAIN (3), and FERGUSON (6) have all figured early stages in mitosis before the fusion of the sex nuclei in *Pinus*. In all of these, however, the sperm nucleus was as active as that of the egg, both nuclei being in approximately the same stage. But in *Atamosco* only the egg nucleus formed a spirem (fig. 16). It soon began to seem strange that there was no increase in the size of the sperm and no evidence of fusion. So more and more material of this stage was cut. In all cases where the pollen tube had entered the sac this condition was seen. More than 600 examples like figs. 12–15 were found, and about half as many in which the spirem in all stages is formed in the egg nucleus (fig. 16). Two-celled embryos show no trace of this sperm nucleus (fig. 27); and a few spindles and telophase stages of this division also give no trace of it.

Then young ovaries were cut to get the development of the sac. But not many had been collected and no satisfactory chromosome count could be made. In one ovary the third mitosis was in progress, but unfortunately the material was not well fixed, some plasmolysis having taken place. Yet in two nuclei of the metaphase stage more than 12 chromosomes were certainly present; but in both instances the nuclei were in the chalazal end of the sac; so this might only mean a repetition of the condition STRASBURGER (25) found in *Lilium Martagon*, of which he says:

> Die Schwesterchromosomen bei der homöotypischen Teilung des im Chalazaende der Embryosakanlage (die hier direkt aus der Embryosakmutterzelle hervorgeht) befindlichen Kerns, statt wie sonst, ohne Längsspaltung in die Kernspindel eingefügt zu werden, eine solche Längsspaltung, wie bei

einem typischen Teilungeschritt erfahren, was eine Verdoppelung der Chromosomenzahl zur Folge bat.

This was the state of the problem when I left Bonn.

A new collection was made this last autumn. Even from this collection the division of the mother cell has not been obtained. As was stated above, the development of the sac must go on very rapidly, for in some ovaries certain ovules are in the mother cell stage while others have mature sacs; and these seem not to be related to any part of the ovary or to follow in any special succession; they occur apparently without any order. The buds appear at the surface of the soil one day with the mother cell undivided and the flowers are open the next and usually last only one day; so the whole development must go on very rapidly.

There is no evidence that permanent walls came in at the division of the mother cell. The two-nucleate sac (fig. 5) never shows any evidence of disintegrating megaspores; so it belongs to the *Lilium* type described by COULTER and CHAMBERLAIN (**5,** p. 73), in which these two nuclei are the daughter nuclei without separating walls, and the nuclei of the four-nucleate sac are the four megaspore nuclei without separating walls. A discussion of this question was given in the paper on *Cypripedium* (**19**), and also by COULTER (**4**). A recent paper by BROWN and SHARP (**2**) shows this condition, and the same view is presented.

The third division in the sac I was fortunate enough to get in nearly all the ovules of one ovary. In many of these the chromosomes were quite distinct and several counts were made (figs. 6, 7, 9). In all cases approximately 24 chromosomes could be counted. The sporophyte number is 24 (fig. 8); therefore the reduction division seems not to have taken place. This gives the egg the sporophyte or diploid number of chromosomes; and, according to STRASBURGER'S definition, when such an egg develops an embryo without fertilization it is a case of apogamy. He says (**26,** p. 80):

> Daher ich das Kriterium für echte Parthenogenesis in der Weiterentwicklung eines Geschlectsproduktes erblickte, das mit der ihm normal Zukommenden haploiden Chromosomenzahl anhebt. Wenn ein diploides Ei einen keim bildet, so bezeichnete ich dessen Entwicklung als Apogam, das Ei selbst als apogames Ei.

He also says that such a diploid egg is in reality already fertilized,

> und zwar in dem Sinne, dass der Zustand, den die Befruchtung in seiner Mutterpflanze schuf, in ihm noch fortdauert, da er nicht durch den Vorgang der Reduktionsteilung, gewissermassen durch Entfruchtung, aufgehoben wurde.

It is already from its organization endowed with the double number of chromosomes, so it goes on, so far as the chromosome number is concerned, developing like the cells of a bud or an adventive embryo. The development of these *Anlagen* would hardly be compared to genuine parthenogenesis, in spite of the fact that no fertilization takes place here. But WINKLER used a different terminology, based on a somewhat different conception, especially with reference to the importance of the haploid or diploid number of chromosomes. He (**29**) would call this "somatic parthenogenesis." He defines parthenogenesis (p. 11) as

> die apomiktische Entstehung eines Sporophyten aus einem Ei, und zwar (*a*) somatische parthenogenesis, wenn das Ei einen Kern mit der diploiden, unreducierten chromosomenzahl besitzt (*b*) generative parthenogenesis, wenn der Kern des Eies mit der haploiden Chromosomenzahl ausgestattet ist.

He defines apogamy as

> die apomiktische Entstehung eines Sporophyten aus vegetative Zellen des Gametophyten, und zwar (*a*) somatische Apogamie, wenn die Zelle oder der Zellkomplex, die den Sporophyten liefern, in ihren Kerne die diploide Chromosomenzahl besitzen (*b*) generative Apogamie, wenn die Kern der Mutterzellen des Sporophyten nur die Haploide chromosomenzahl fuhren.

That is, WINKLER would call the development, without the aid of a male gamete, of an egg (either haploid or diploid) parthenogenesis, the development of vegetative cells (from a gametophyte) apogamy. There can be no question concerning the latter, but there may be a difference of opinion as to whether the development of both diploid and haploid eggs without fertilization should be called parthenogenesis.

In *Atamosco* the organization of the egg, with the exception of the presence of the diploid number of chromosomes, is perfect so far as morphological evidence goes. The whole egg apparatus is characteristically developed, being quite distinct in appearance

from all other cells of the sac. Even the synergids are not to be confused with the egg, each showing its own peculiar characters (figs. 10, 11). It happens that more than one egg is sometimes organized, and apparently all these eggs in *Atamosco*, but no other cell, may function. As all the nuclei of the female gametophyte have the diploid number of chromosomes, it might be thought that any cell could develop a sporophyte, and therefore adventive embryos and polyembryony would be common. But no evidence of adventive embryos was found; and only a few sacs with two embryos were seen, and in every instance they were paralleled in other sacs by an egg in a similar position (figs. 28, 33, 34).

If the egg be considered a diploid gamete, then this should be considered parthenogenesis, but we usually define a gamete as a cell that fuses with another before developing, and it would seem that it should at least be capable of so doing if it is called a gamete. But this egg cell lacks this gamete character; for *Atamosco* seems to show conclusively, not only that it is capable of developing without fertilization, but that it will not fuse with the male gamete although the two nuclei be in contact (figs. 15–24). If this inability to fuse shows that it is really not a gamete, then this is apogamy. It is certainly apogamy if we consider it from the standpoint of the part taken in the process by the male nucleus. Apogamy might be defined as the development of a sporophyte from a diploid egg without fertilization. Vegetative apogamy would be the development of a sporophyte from vegetative cells of the gametophyte, while parthenogenesis would be reserved for the development of a sporophyte from an egg with the haploid number of chromosomes.

In 1900 JUEL (**11**) showed that *Antennaria alpina* has very few staminate individuals, and even these have anthers entirely sterile or only slightly fertile. The megaspore develops without the reduction division. The *Alchemilla* group was investigated by MURBECK (**16**) in 1901 and by STRASBURGER (**23**) in 1905. In the apogamous species the reduction division does not take place in the megaspore development. In the microspore series, in some species, the cells develop no farther than the mother cell stage, others disintegrate after the first division, while still others complete the tetrad division and imperfect pollen is produced. In

1904 OVERTON (**18**) investigated *Thalictrum*, finding the pollen normal. In some instances there was a reduction division in the development of megaspores, while others developed without this, a case exactly parallel to that of *Marsilia* as shown by STRASBURGER (**24**) in 1907. In *Taraxacum officinale* JUEL (**12, 13**) in 1904 and 1905 states that the embryo sac mother cell divides only once, the inner daughter cell developing the sac, but no reduction division takes place. The reduction division does take place in the microspore development.

ROSENBERG (**22**) in 1907 found in *Hieracium* that the reduction division takes place in the microspore development, but in some species, at least, they are disintegrating even at this time, and the mature anthers are empty. In some species the megaspore development is occasionally normal, giving a haploid gametophyte; but it usually happens that some sporophyte cell (epidermal, chalazal, or nucellar cell) produces the embryo sac. So this is a case of apospory in the development of the sac; and as a diploid egg is organized, it is also a case of apogamy in the development of the embryo. The work of WINKLER (**28**) in 1904 and of STRASBURGER (**26**) in 1909 with *Wikstroemia* shows reduction in the microspore development with but little pollen maturing, while reduction does not take place in the megaspore development. In 1910 STRASBURGER (**27**) added *Elatostema* to the apogamous angiosperms. It also has the reduction in the pollen development with much irregularity in the pollen, some anthers producing pollen of normal appearance. The mother cell of the ovule begins the reduction division but returns to the vegetative mitosis; but in some cases reduction does take place. From these it seems that reduction always takes place in the microspore development, the failure being only in the megaspore series, and in some species it is only partial here.

It will be seen that normal pollen is reported only for *Thalictrum*, some species of *Taraxacum*, and *Atamosco*, the others all having little pollen or defective pollen. The female gametophytes for four genera are diploid, while in the other three both haploid and diploid female gametophytes are developed; but it is not known that these haploid eggs develop parthenogenetically. According to

YAMANOUCHI (30) this is true for the fern *Nephrodium*, which develops a haploid sporophyte from a haploid unfertilized egg.

SUMMARY OF APOGAMOUS ANGIOSPERMS

	Pollen	Female gametophyte
Urticaceae		
Elatostema	Defective	Diploid or haploid
Ranunculaceae		
Thalictrum	Normal	Diploid or haploid
Rosaceae		
Alchemilla, Eualchimilla	Defective	Diploid
Thymelaeaceae		
Wikstroemia	Little	Diploid
Compositae		
Antennaria	Little	Diploid
Taraxacum	Normal or little	Diploid
Hieracium	Little	Haploid or diploid
Amaryllidaceae (Leucojaceae)		
Atamosco	Normal	Diploid

STRASBURGER (24) holds that a diploid egg not only is not fertilized, but is not capable of being fertilized. He says (p. 166):

> Womit kann nämlich das apogame Ei einer *Marsilia* besser beweisen, dass es weder Befruchtungsbedurftig noch Befruchtungsfähig ist, als dass es den Spermatazoiden den Eintritt in das Archegonium unmöglich macht? Die diploide Chromosomenzahl bedingt es also, dass im Ei dass Befruchtungsbedürfnis sich nicht einstellt und damit auch der Reiz wegfällt, der die Tätigkeiten sonst anlöst, ist welche die Befruchtung vorbereiten. Also kommt doch wohl eine grundsätzliche Bedeutung an dieser Tatsache zu, dass nicht die einfache, sondern die doppelte Chromosomenzahl im Kern vertreten ist.

In the apogamous *Marsilia* the canal cell does not disintegrate, so that the sperm cannot enter the archegonium. STRASBURGER'S idea of the incapability of the fertilization of the diploid egg was worked out on theoretical grounds altogether, as is shown in the quotations just given, and as he said in discussing this question with me.

OVERTON (18, p. 278) says that in pollinated material he often found pollen tubes in the micropyles of ovules and even in contact with the egg, and also the fusing of the second sperm nucleus with the endosperm nucleus. But his preparations failed to show the fusion of the sperm and egg nuclei, and he adds:

An diesem Grunde darf ich auch nicht positiv behaupten, dass zur normalen Keimentwicklung stets Befruchtung notwendig ist, wenn auch alle sonstigen Tatsachen und die Beobachtungen an Pflanzen im Freien kienen Zweifel darüber lassen, dass Befruchtung stattfinden kann, wenn das Ei die reduzierte Zahl der Chromosomen führt.

In *Atamosco* I have been able to settle this question beyond a doubt I think; for about 30 cases of an egg dividing with the sperm inactive although in contact, or nearly so, with the egg nucleus were examined. The sperm gradually disintegrates (figs. 18, 21–24, 27) and evidently the egg is incapable of fusing with the sperm, the latter being perfectly normal in every way so far as appearances go, for the sperm had the haploid number of chromosomes, and the pollen seemed entirely normal, and pollen tubes enter the sac in the usual way. The other sperm does fuse with the polars either before or after their fusion. This would seem to show that the triple fusion is not of the same character as that which takes place when the sperm and egg fuse. So *Atamosco* seems to prove STRASBURGER's theory that the diploid egg is incapable of fertilization.

On the completion of the work, I reported to Professor STRASBURGER what I had found, and in his reply, received February 25, 1912, he says:

Die Schwerpunk Ihrer Arbeit wird darin liegen, dass der Eikern, weil er doppeltchromosomig ist, die Aufnahme dem Spermakern versagt, ungeachtet die übrigen Einrichtungen bei der Pflanze fortbestehen, die den Spermakern bis in das apogame Ei hineinführen.

Summary

1. The pollen is normal. The haploid number of chromosomes is 12.

2. The third division in the embryo sac shows the diploid number of chromosomes to be 24.

3. Usually the ordinary 8-nucleate sac is organized, but occasionally antipodals organize in the micropylar end and the egg apparatus at the side of the sac, sometimes more than one egg organizing.

4. Two male nuclei come into the sac with the pollen tube, one

fusing with the two polars, the other entering the egg but never fusing with it, and finally disintegrating during the first division in the egg.

5. A diploid egg seems to be incapable of fertilization.

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LITERATURE CITED

1. BLACKMAN, V. H., On the cytological features of fertilization and related phenomena in *Pinus silvestris*. Phil. Trans. Roy. Soc. London B **190**: 295–427. *pls. 12–14*. 1898.
2. BROWN, W. H., and SHARP, L. W., The embryo sac of *Epipactis*. BOT. GAZ. **52**: 439–452. *pl. 10*. 1911.
3. CHAMBERLAIN, C. J., Oogenesis in *Pinus Laricio*. BOT. GAZ. **27**: 268–281. *pls. 4–6*. 1899.
4. COULTER, J. M., Relation of megaspores to embryo sacs in angiosperms. BOT. GAZ. **45**: 361–366. 1908.
5. COULTER, J. M., and CHAMBERLAIN, C. J., The morphology of angiosperms. 1903.
6. FERGUSON, M. C., Life history of *Pinus*. Proc. Wash. Acad. Sci. **6**: 1–202. *pls. 2–24*. 1904.
7. GUIGNARD, L., Sur les anthérozoides et la double copulation sexuelle chez les végétaux angiospermes. Compt. Rend. **128**: 864–871. *figs. 19*. 1899.
8. ———, Étude sur les phénomènes morphologiques de la fécondation. pp. 100–147. *pls. 2–5*. 1889.
9. ———, La double fécondation chez les Renonculacées. Jour. Botanique **15**: 394–408. *figs. 16*. 1901.
10. ———, La double fécondation chez les Solanées. Jour. Botanique **16**: 145–167. *figs. 45*. 1902.
11. JUEL, H. O., Verleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung *Antennaria*. Kgl. Svensk. Vetensk. Akad. **33**: no. 5. pp. 59. 1900.
12. ———, Die Tetradenteilung in der Samenanlage von *Taraxacum*. Arkiv f. Bot. **2**: no. 4. 1904.
13. ———, Die Tetradenteilungen bei *Taraxacum* und anderen Cichoraceen. Kgl. Svensk. Vetensk. Akad. **39**: no. 4. 1905.
14. LAND, W. J. G., Double fertilization in Compositae. BOT. GAZ. **30**: 1–11. *pl. 1*. 1900.
15. MODILEWSKI, J., Zur Embryobildung von *Euphorbia procera*. Ber. Deutsch. Bot. Gesells. **27**: 21–26. *pl. 1*. 1909.

16. MURBECK, Sv., Parthenogenetische Embryobildung in der Gattung *Alchemilla*. Lunds. Univ. Arrsskr. **36**: no. 7. 1901.
17. NAWASCHIN, S., Über die Befruchtungsvorgänge bei einigen Dicotyledoneen. Ber. Deutsch. Bot. Gesells. **18**: 224–230. *pl. 9*. 1900.
18. OVERTON, J. B., Über Parthenogenesis bei *Thalictrum purpurascens*. Ber. Deutsch. Bot. Gesells. **22**: 274–283. 1904.
19. PACE, L., Fertilization in *Cypripedium*. BOT. GAZ. **44**: 353–374. *pls. 24–27*. 1907.
20. ———, The gametophytes of *Calopogon*. BOT. GAZ. **48**: 126–137. *pls. 7–9*. 1909.
20a. ———, *Parnassia* and some allied genera. Bot. Gaz. **54**: 306–329. *pls. 14–17*. 1912.
21. PORSCH, O., Versuch einer phylogenetischen Erklärung des Embryosackes und der doppelten Befruchtung der Angiospermen. Jena. 1907.
22. ROSENBERG, O., Cytological studies on the apogamy in *Hieracium*. Bot. Tidsskr. **28**: 143–170. 1907.
23. STRASBURGER, E., Die Apogamie der Eualchimillen und allgemeine Gesichtspunkte, die sich aus ihr ergeben. Jahrb. Wiss Bot. **41**: 88–164. 1905.
24. ———, Apogamie bei *Marsilia*. Flora **97**: 123–191. *pls. 3–8*. 1907.
25. ———, Chromosomenzahlen, Plasmastrukturen, Vererbungsträger, und Reduktionsteilung. Jahrb. Wiss. Bot. **45**: 1908.
26. ———, Zeitpunkt der Bestimmung des Gaschlects, Apogamie, Parthenogenesis, und Reduktionsteilung. Hist. Beiträge **7**: 1–124. *pls. 1–3*. 1909.
27. ———, Sexuelle und apogame Fortpflanzung bei Urticaceen. Jahrb. Wiss. Bot. **47**: 245–288. *pls. 7–10*. 1910.
28. WINKLER, H., Über Parthenogenesis bei *Wikstroemia indica*. Ber. Deutsch. Bot. Gesells. **22**: 573–380. 1904.
29. ———, Parthenogenesis und Apogamie in Pflanzenreich. pp. 162. *figs. 14*. 1908.
30. YAMANOUCHI, S., Apogamy in *Nephrodium*. BOT. GAZ. **45**: 289–318. *pls. 9–10*. 1908.

EXPLANATION OF PLATES XIII AND XIV

All figures were drawn with a camera lucida. The magnification given is that of the original drawings, which are reduced one-half in reproduction. The abbreviations used are as follows: *e*, egg; *g*, generative nucleus; *m*, male nucleus; *p*, pollen tube; *s*, synergid; *t*, tube nucleus.

FIG. 1.—Pollen grain: tube nucleus (amoeboid) and generative nucleus with 12 chromosomes; ×1000.

Fig. 2.—A spirem in the generative nucleus, from the same anther; ×1000.

FIG. 3.—A germinating pollen grain from the stigma; the generative nucleus in advance of the tube nucleus and in mitosis; ×400.

FIG. 3, *a*.—The generative nucleus from fig. 3; ×1000.

FIG. 3, *b*.—The remainder of the above nucleus from the adjacent section; chromosomes show longitudinal splitting; 12 chromosomes in *a* and *b;* ×1000.

FIG. 4.—Diagram of young ovule showing mother cell; ×600.

FIG. 5.—Two-nucleate sac; daughter nuclei without separating walls; ×400.

FIGS. 6 and 6, *a*.—Two adjacent sections of the same sac; both nuclei of micropylar end of sac in anaphase stage; in each spindle 24 chromosomes can be counted at one end; an accurate count at the other end is not possible; ×1000.

FIG. 7.—Metaphase at chalazal end of four-nucleate sac with 24 chromosomes; ×1000.

FIG. 8.—A somatic cell from ovule walls in metaphase, showing 24 chromosomes; ×1000.

FIG. 9.—Telophase of the third division of the sac; remains of previous spindle; the uncut spindle of the present division shows the beginnings of wall formation; the cut spindle is perpendicular to the section, so only one end of it is shown; this nucleus shows approximately 24 chromosomes; ×1000.

FIG. 10.—The egg apparatus from mature sac; filiform apparatus well developed, but no notch in the synergids; ×1000.

FIG. 11.—Antipodal end of sac; polars in contact; ×400.

FIG. 12.—Micropylar end of sac after pollen tube enters; ×600.

FIG. 13.—Micropylar end of the sac; ×1000.

FIG. 13, *a*.—Primary endosperm of same sac before triple fusion is complete; ×1000.

FIG. 14.—Egg and male nucleus almost in contact; ×1000.

FIG. 14, *a*.—Triple fusion from same sac; ×1000.

FIG. 15.—Micropylar end of sac; ×600.

FIG. 16.—Egg nucleus with well developed spirem and male nucleus near it; ×1000.

FIG. 17.—Egg nucleus showing approximately 24 chromosomes; male nucleus near it; ×1000.

FIG. 18.—Micropylar end of sac; egg nucleus with approximately 24 chromosomes; the nuclear membrane has disappeared; ×1000.

FIG. 19.—Egg nucleus similar to that in fig. 17; ×1000.

FIG. 20.—Egg nucleus similar to that in fig. 18, but sperm still has nuclear membrane; ×1000.

FIG. 21.—Spindle beginning to organize in the egg; male nucleus very dense; ×1000.

FIG. 22.—Metaphase in the egg nucleus; nuclear membrane of the male nucleus breaking down; 1000.

FIG. 23.—Anaphase in egg nucleus; male nucleus has approximately 12 chromatic masses, apparently chromosomes; ×1000.

FIG. 24.—Micropylar end of sac; male nucleus very close to spindle of egg nucleus, which is in anaphase stage; ×600.

FIG. 25.—Undivided egg with about 64-nucleate endosperm; other sacs in this ovary have embryos of about 16 cells; pollen tube contains three nuclei; ×600.

FIGS. 26, 26, *a*, and 26, *b*.—Three sections of the same endosperm nucleus in metaphase; ×1000.

FIG. 27.—Two-celled embryo with pollen tube entering one synergid; ×600.

FIG. 28.—Micropylar end of sac with two eggs and no synergids; ×600.

FIG. 29.—Diagram of sac with three, possibly five, eggs, one antipodal, and two fusing polars; ×105.

FIG. 30.—One antipodal in the usual position, the group of six nuclei in the micropylar end of the sac having the appearance of antipodals; a perfect egg apparatus is organized on one side; one cell near the antipodal region has the egg organization, and four nuclei are fusing in the upper end of the sac; ×105.

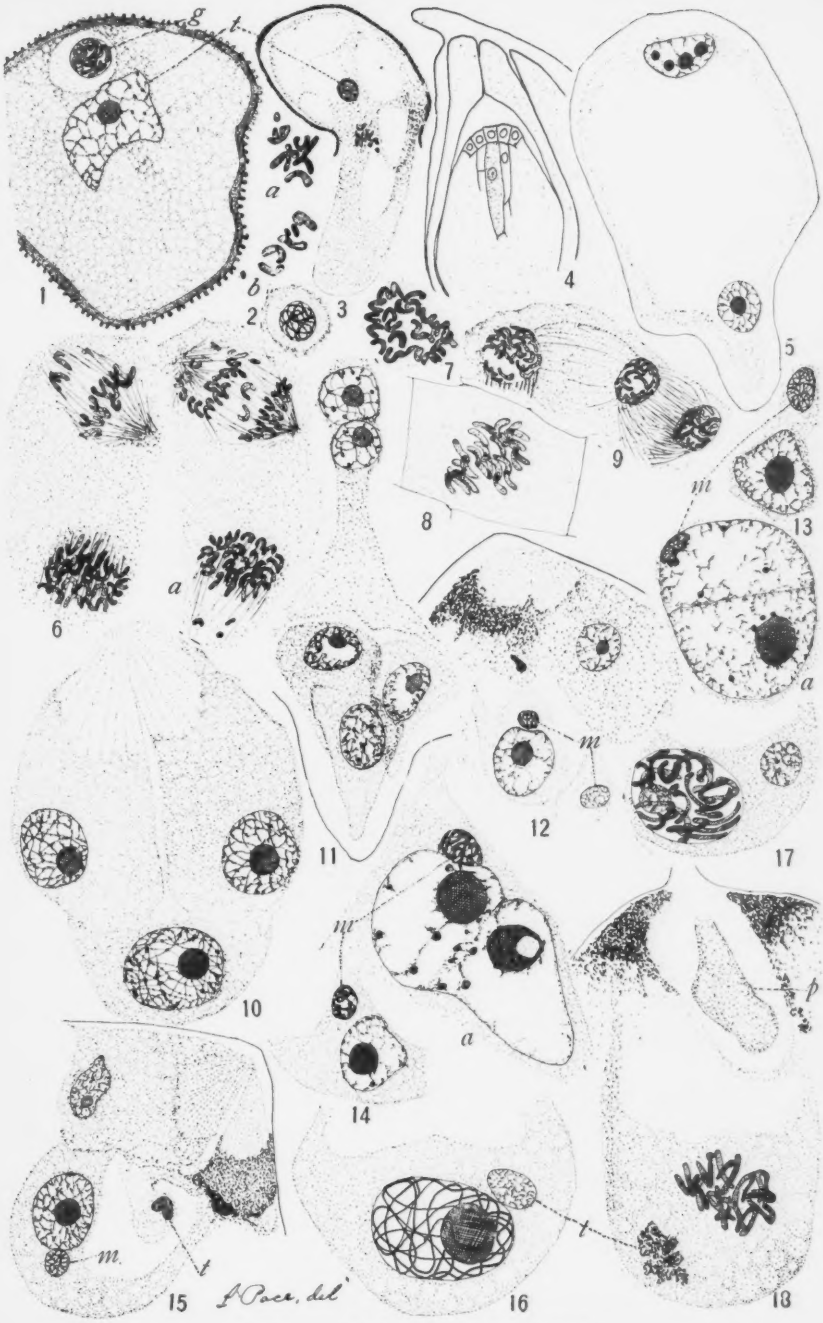
FIG. 31.—Egg apparatus slightly to one side, showing male nucleus in the egg, behind and just in contact with the nucleus; ×600.

FIG. 32.—Egg apparatus of four nuclei near the antipodal region; pollen tube entering; ×1000.

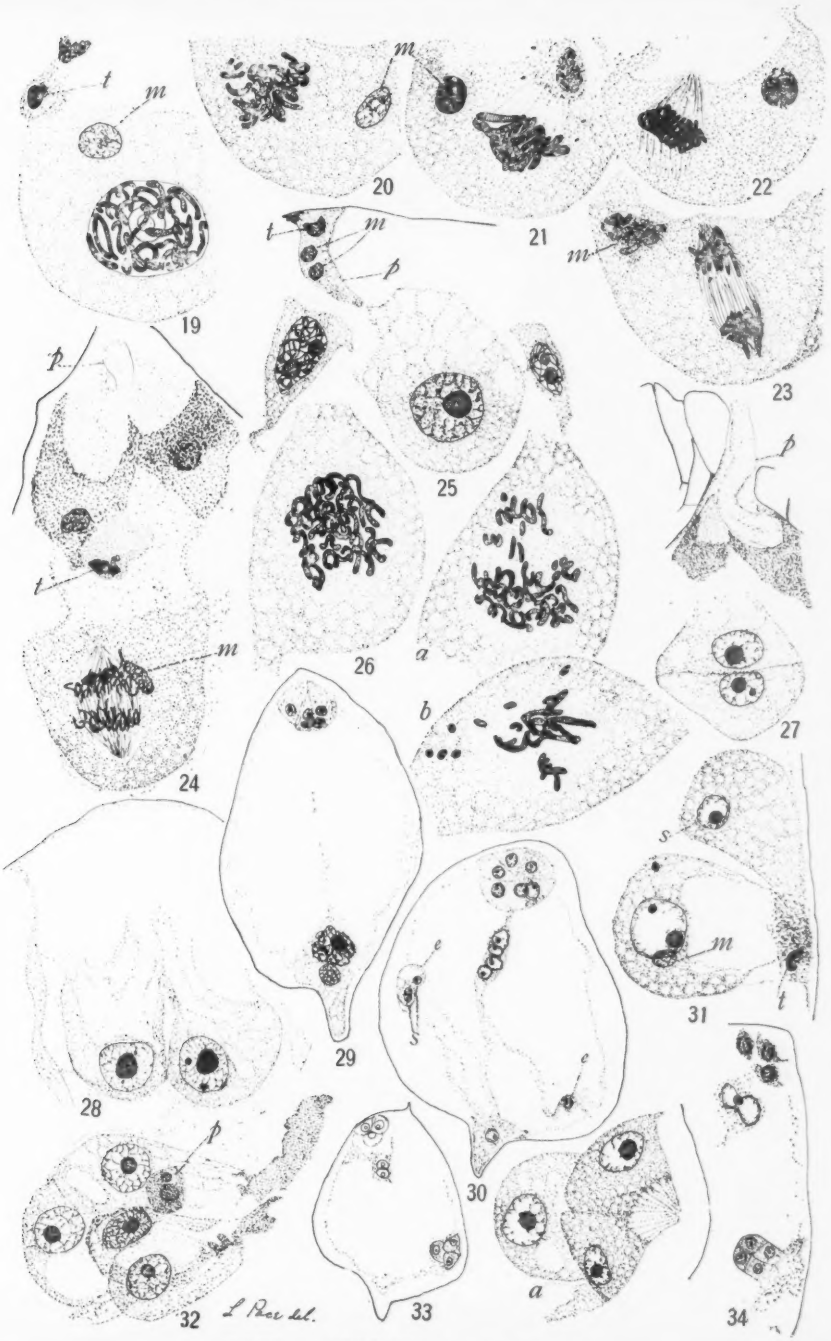
FIG. 33.—The very common type of abnormal sac except that the antipodals are not exactly at the micropylar end of this sac; ×105.

FIG. 33, *a*—Egg apparatus of the same sac; ×600.

FIG. 34.—Four-celled embryo from a side egg; primary endosperm nucleus still undivided; ×105.



PACE on APOGAMY IN ATAMOSCO



PACE on APOGAMY IN ATAMOSCO

THE TEPARY, A NEW CULTIVATED LEGUME FROM THE SOUTHWEST

GEORGE F. FREEMAN

(WITH ELEVEN FIGURES)

The great aridity and extreme heat of the southwestern part of the United States have developed a flora singular in type and striking in contrast with such as is found in the more humid sections. So widely distinct are the atmospheric conditions that none but the hardiest and most adaptable of introduced plants are able to withstand the violent readjustment made necessary by the new environment, even though water in abundance be artificially supplied. Professor J. J. THORNBER of this station is authority for the statement that only a small percentage of plants or varieties developed in sections having a decidedly different climate from that of Arizona may be successfully cultivated here.

Alfalfa, which has been grown within the territory for many years, is now thoroughly acclimatized and is today our greatest single farm product. Among other crops introduced since the European settlement of Arizona and southern California and thoroughly acclimatized may be mentioned barley, the white Sonora wheat, the olive, pomegranate, and several varieties of figs, dates, and citrus fruits. Realizing that the plants which are most successful in resisting the vicissitudes and appropriating the peculiar advantages of the climate of Arizona are those which have been longest grown within its borders, the writer has had his attention drawn to some of the native economic plants of this region. Among these may be found varieties of agricultural plants which have been grown within the confines of Arizona for hundreds or perhaps even thousands of years, years when the ruins that now crumble in the desert sands were populated with a happy and prosperous race, years when the canal systems which still can be distinctly traced ran on higher levels and watered more lands than those which at the present time distribute the waters of the Gila and Salt rivers. Here among the Pima and Papago Indians, descendants

or successors of these former builders, may be found varieties of corn, beans, pumpkins, and squashes which have survived the race under whose husbandry they were produced. Centuries of adaptation have therefore produced types eminently suited to withstand the extremes of heat and drought to which the climate and indifferent agriculture of a primitive people often exposed them.

The investigations of which this paper forms a report are concerned with the varieties of native beans only. The need for a leguminous food plant to restore nitrogen to soils irrigated with pumped water, and the necessity of finding drought-resistant crops suitable for use where "dry-farming" is being attempted, has directed the attention of the Arizona Experiment Station to these beans for several years. Tests at Yuma under irrigation, and at McNeal under dry farm conditions, have already demonstrated the ability of these native beans to fulfil all of the requirements of drought-resistance and fertilizing value, and in addition they have the ability to produce profitable crops of a staple product.

During these agricultural tests, made for the most part from seeds secured originally from the Indians, it was noticed that many apparently different sorts occurred. In order to study the different varieties in their native condition, therefore, and to secure samples for testing their relative values, the writer in company with Director FORBES spent two weeks during late July and early August 1910 among the Papago Indians in their villages situated in the valley between the Baboquivari and Quijotoa mountains, some 50–100 miles southwest of Tucson. Here, in a region with 9 inches of rainfall annually, these beans were being grown successfully with no irrigation save that of a little flood water which came down the mountain washes.

During the course of this trip 32 samples of beans were secured. In addition to these, 10 samples had been previously secured by Mr. CAVILLO from the Papago Indians near Santa Rosa and grown one year at Yuma; 7 samples were furnished by Professor J. J. THORNBER from beans secured from the Pimas at Sacaton; some 25 carefully selected samples were contributed by Mr. MENAGER, of the Indian Oasis, which he picked from beans secured from the Papagos, and finally, as a result of a three days' trip among the

Pimas at Sacaton, 16 additional samples were secured. This mass of material when carefully sorted yielded 71 apparently distinct sorts. These were planted on the testing grounds at the university during the summer of 1910 and produced strains of the most widely diverse types and economic values.

The first lot of seed coming into the hands of the writer were 10 samples obtained originally from Mr. CAVILLO at Santa Rosa, but which had been grown for one year at the Experiment Station at Yuma. In working over this material two distinct types were observed. The first type was characterized by a larger size, averaging about 0.23 gm. When present at all, the markings or flecks were much coarser; there was an absence of lines radiating from the hilum, such as are used by botanists to distinguish between the kidney and lima beans. Another distinguishing characteristic of this group was the smoother, more glistening surface of the seed coat. The second type averaged distinctly smaller (about 0.15 gm.); the markings or flecks when present were much finer; distinct lines radiating from the hilum were frequently present; the surface of the seed coat lacked the characteristic glossiness of the first type. Inquiry soon developed the fact that Indians and Mexicans of southern Arizona and Sonora distinguish sharply these two classes, the latter designating the first type as "frijoles" and the second as "teparies." It is interesting to note that they think of these two legumes as being quite as distinct as we should think of rye and wheat. After once becoming familiar with the differences between the two types, anyone recognizes without hesitation and at a glance whether any given sample is composed of teparies or frijoles, in spite of the fact that previously he may never have seen that particular variety.

Frijoles

The common frijole undoubtedly belongs to *Phaseolus vulgaris* Linn. The Papago equivalent of the bean is *mōn*. They call a certain yellow bean *sōam mōn* (*sōam*=yellow, *mōn*=bean). In like manner they call the pink bean *yura mōn*. The word *yura* is of Yaqui origin and is said to refer here to the white man rather than to the color of the bean, thus meaning "the white man bean."

This also accords with the Indian tradition that beans had been secured from the white man, but that they had grown teparies "long time." Distributional and other evidence also points to the more southern origin of beans, which in all probability were brought northward by the earlier Spanish settlers and missionaries.

Teparies

The name tepary or *tepari* (Spanish) originated from the Papago words *stäte päve; stä-te* meaning white and *päve* having reference to the kind of plant to distinguish it from the *mõn* or bean. In like manner they speak of *sõam* (yellow) *päve* and *späte mõõk* (muddy) *päve*. In addition to the very common statement, above quoted, that they (the Indians) had secured beans from the white man, but had grown *päve* a long time, several of the old men and women of the Papago tribe in widely separated villages gave the strikingly uniform answer that their forefathers got teparies from a people which had once inhabited that region (the Baboquivari and Quijotoa district of southern Arizona), and had grown these beans in the same valleys where they are now grown, but that these people went away "long ago." However, two different old women said that they remembered having gathered dark colored wild teparies during their childhood in the mountains farther south (presumably in Sonora). It is a common statement by Mexicans that the yellow tepary grows wild in Sonora and makes vines like a morning glory in the damp soil of canyons. Weight is further given to these statements and traditions concerning the local origin of these varieties by the greater resistance of teparies to extremes of climate than is possessed by beans. Adaptation through a longer series of years, or perhaps, as the present evidence seems to indicate, even domestication from the wild state in the same localities where now grown, has rendered them more hardy than the exotic beans. When the irrigating water or rains fail, teparies will frequently make a good crop when beans are a total failure. In a field of red Indian beans belonging to a Pima Indian near Sacaton in the fall of 1910, in which the crop was a total failure on account of an insufficient water supply, the writer noted a few yellow tepary plants growing as an admixture among the beans. Under conditions such

FIG. 1.—Tepary above, bean below: both planted May 17, photographed August 20; tepary producing abundantly; bean crop total failure on account of heat; leaves removed to show presence or absence of pods.

that the most vigorous of the beans had produced but two or three pods, some of the tepary plants had as many as 200 ripe pods and the average was more than 100. During 1911 pink beans which were planted May 17 had not bloomed on account of the heat as late as August 20, although they have been well irrigated during that time (fig. 1). Teparies planted alongside the beans on the same day and given identical treatment had by that time ripened an abundant crop of seed. It is a common statement among the Pima Indians that when the beans are destroyed by insects the teparies go free.

It has now been noted that the traditional origin of the bean and the tepary are distinct, that physiologically the tepary differs from the bean in being more resistant to heat, drought, and insect attack, and hence is more productive in hot regions. It remains yet to describe those morphological distinctions which compel the conclusion that the tepary does not belong to the same species as does the kidney bean.

Characters of the tepary

The characters of tepary are best indicated by contrasting them with those of the kidney bean (*Phaseolus vulgaris*) and the lima bean (*P. lunatus*). The seeds are smaller, averaging about 0.15 gm. instead of about 0.23 gm. for beans and 0.50 gm. or more for limas. When present at all, the markings or flecks on teparies are much finer than on the other two. The seed coat of the tepary lacks the characteristic glossiness of the kidney bean.

The length of the petioles of the first pair of aerial leaves are strikingly different in the tepary and the varieties of *P. vulgaris* and *P. lunatus*. Measurements of the mature petioles of the first pair of aerial leaves on a large number of seedling of several varieties of each gave for the average of the tepary 4.3 mm., for beans 24.33 mm., and for the limas 43.7 mm. The first pair of aerial leaves of all three species are simple, but those of the tepary differ from the others in having truncate instead of cordate bases (figs. 2 and 3). They are also smaller and narrower, the averages being as shown in table I.

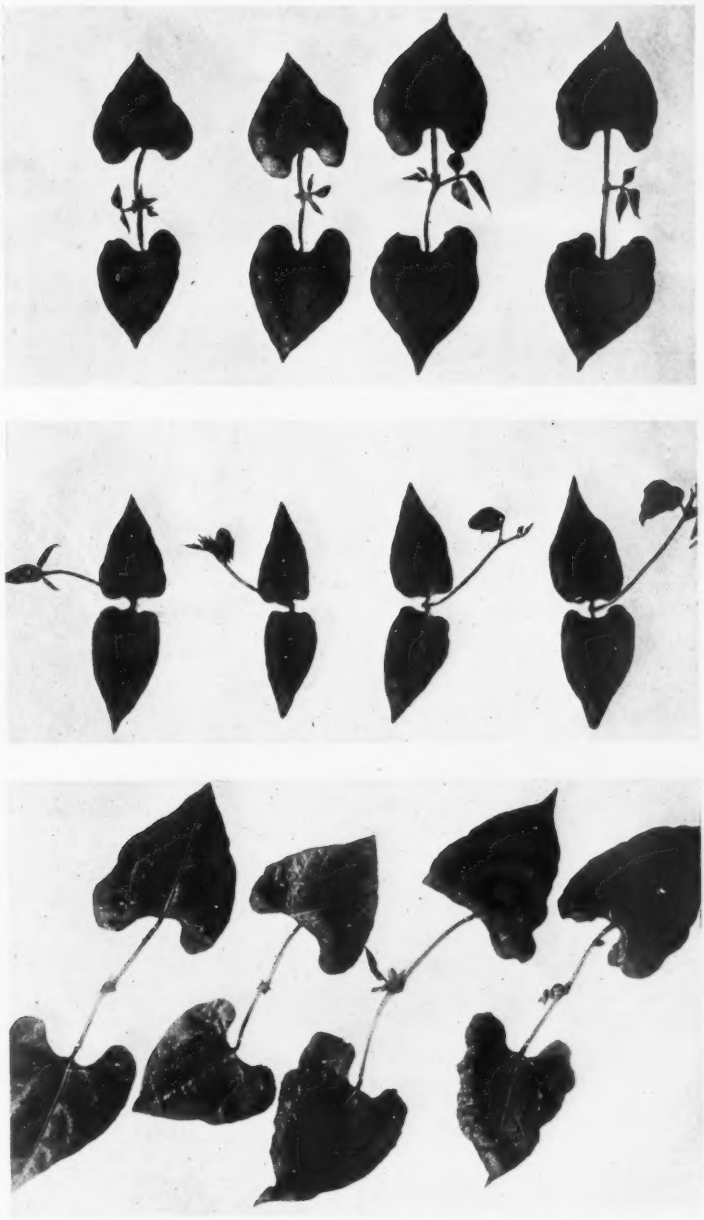
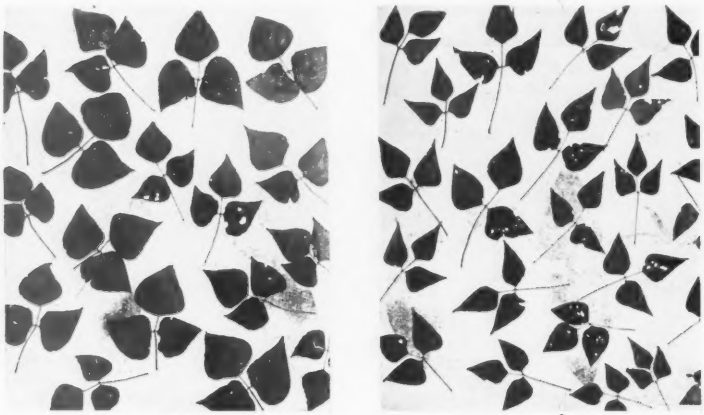


FIG. 2.—Seedlings showing first pair of aerial leaves; top, bean; middle, tepary; bottom, lima bean.

TABLE I

	Av. length mm.	Av. width mm.	Ratio $\frac{W.}{L.}$
Tepary	55.12	33.14	1.67
Kidney bean	47.32	45.86	1.01
Lima bean	72.80	66.89	1.08

The apices of all the leaves of the tepary are more acute than those of either the kidney or lima beans, and they are also much smoother (not crumpled and rough).



a *b*

FIG. 3.—Typical leaves of bean (*a*) and tepary (*b*)

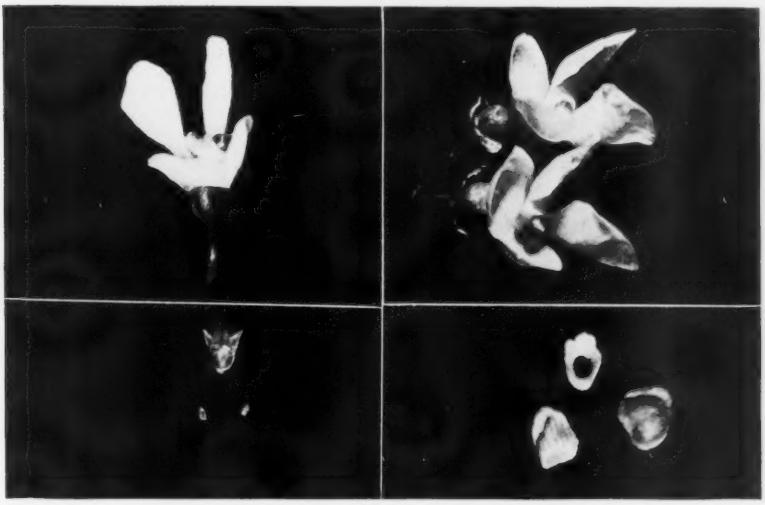
The length and breadth of the terminal leaflets of 100 normal mature leaves taken at random and including several varieties each of both beans and teparies were measured with the following results:

TABLE II

	Av. length mm.	Av. breadth mm.	Ratio $\frac{L.}{B.}$
Teparies	63.80	36.59	1.74
Beans	78.80	64.70	1.21

The flowers of the tepary are smaller than those of the bean, the wings are narrower in comparison with their length, and the

banner is more strongly reflexed in flower. The calyx tube is deeper in the tepary, and the two upper teeth are united to form one prominent acuminate tooth rather than being separate and nearly obscure as in the bean. The lower three teeth of the calyx tube of the tepary are also much longer and more tapering than those of the bean, being described as acuminate rather than acute triangular to obtuse or rounded as in the latter species (fig. 4). The bracts subtending the calyx of the bean are large and nearly



a *b*

FIG. 4.—Flowers of tepary (*a*) and bean (*b*) above; dissected calyx tube and bracts of each below.

orbicular, measuring about 5 mm. in either direction. The corresponding bracts of the tepary are exceedingly small, inconspicuous, and early deciduous. They are lanceolate in outline and are about 1.5 mm. long by 0.5–0.66 mm. broad. In this respect the tepary resembles the lima bean. The flower of the lima differs from that of the bean or tepary in having its banner of a different texture and color from the wings, since it contains chlorophyll and is a pale greenish-yellow color with a purple tinge, whereas the banner of the other two species is either white or colored in the normal way.

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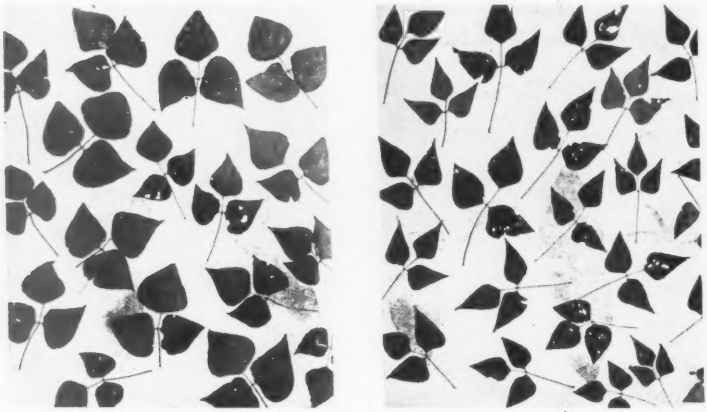

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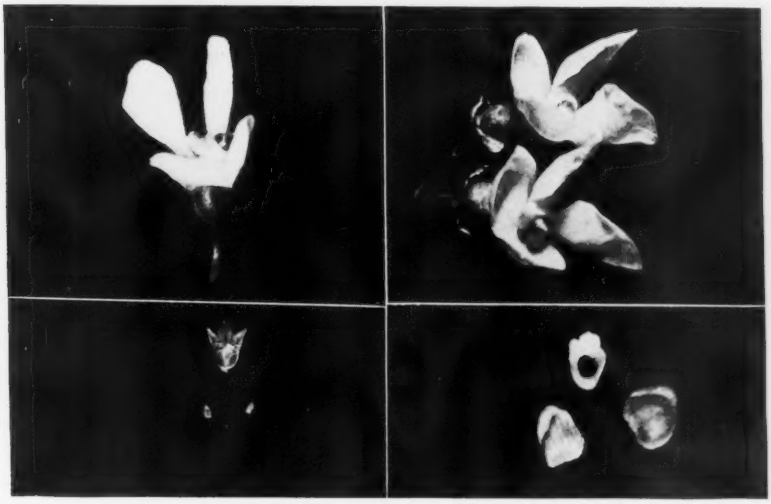

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In all three species, at the opposite side of the hilum from the micropyle, the raphe ends with a more or less prominent elevation. In beans and teparies this elevation is completely divided into two lobes by a crease beginning at the hilum and passing between them. In the limas, on the other hand, the crease enters the elevation but does not pass entirely through it. The raphe of the lima therefore ends in a V-shaped, two-pronged elevation rather than in two rounded, completely separated elevations as in the other two species (fig. 5). The character generally used in botanical keys to distinguish between the lima and kidney bean is the presence of vascular lines radiating from the hilum. These are distinctly visible in the former, but lacking in the latter species. This character is very variable in the tepary, being prominent in some varieties and entirely wanting in others, with every degree of variation between these extremes.

FIG. 5.—Ventral view of lima bean (*a*), bean (*b*), and tepary (*c*).

Since the tepary does not belong to either of the species which include the varieties of the kidney and lima beans, the question arises whether it has heretofore been recognized among the domesticated beans.

In the monographs of JARVIS[1] and IRISH[2] on the garden beans, five genera are recognized: *Phaseolus* (kidney bean), *Vicia* (broad, English, or Windsor beans), *Vigna* (cowpea), *Dolichos* (asparagus bean), and *Glycine* (soy, soja, or coffee bean). To these TRACY[3] adds macunna (velvet bean).

The economic species of *Phaseolus*, according to each of these writers, are three:[4] *P. vulgaris* (kidney bean), *P. lunatus* (lima

[1] JARVIS, C. D., American varieties of beans. Cornell Bull. 260. pp. 149–245. 1908.

[2] IRISH, H. C., Garden beans cultivated as esculents. Missouri Bot. Gard. Ann. Rept. 12. pp. 81–165. 1909.

[3] TRACY, W. W., JR., American varieties of garden beans. U.S. Dept. Agric., Bur. Pl. Ind. Bull. 109. pp. 5–173. 1907.

[4] The seven species of common bean (*P. vulgaris* Savi, *P. compressus* Martens, *P. gonospermus* Savi, *P. carinatus* Martens, *P. oblongus* Savi, *P. ellipticus* Martens, and *P. sphaericus* Martens), which were separated by GEORGE VON MARTENS (*Die Gardenbohnen*. 1860) according to the shape and size of the seed, are now recognized as varieties of *P. vulgaris* L.

bean), and *P. multiflorus* (runner bean). BAILEY[5] states that the moth bean (*P. aconitifolius* Jacq.) is cultivated as a human food in India, and that *P. Mungo* Linn., with its vars. *glaber* Roxberg (adzuki bean) and *radiatus* Hook., are widely cultivated in southern Asia. It has already been shown that the tepary differs specifically from *P. vulgaris* and *P. lunatus*. It may now be distinguished from *P. multiflorus*, *P. aconitifolius*, and *P. Mungo* by the following characters:

TABLE III

	Tepary	*P. multiflorus*	*P. aconitifolius*	*P. Mungo*
Leaflets..	Simple	Simple	2–3 lobed at apex	Simple
Flowers..	4–5, small, at the end of raceme which is generally inferior to the leaves	Large and showy, in many-flowered racemes	Very small, yellowish, in heads at the ends of axillary peduncles	Rather small, yellowish, in a capitate cluster of 5 or 6 on the end of stout hairy axillary peduncles
Stem	Nearly smooth or slightly puberulent	Minutely pubescent	Brown hairy	Densely clothed with long brown hairs

Since it is evident that the tepary does not belong to any of the species now recognized as cultivated esculents or ornamentals, there remains to compare it with the described wild species. The *Index Kewensis* lists 141 species of *Phaseolus*, of which 90 are indigenous to North and South America and the adjacent islands. ROSE[6] states that "nearly 50 species of *Phaseolus* have been reported from Mexico and Central America, and I have no doubt but many remain yet undescribed." Upon going over the available literature I have been able to find 54 species recorded as growing in the southwestern United States, Mexico, and Central America. Indian tradition states that the tepary has been grown within its present habitat since prehistoric times. The physiological evidence from the hardiness and drought-resistance of these plants supports this view. It is more than likely, therefore, that this species was domesticated from wild plants growing within this region or adjacent Mexico rather than from species indigenous to moist tropical

[5] BAILEY, L. H., Cyclopedia of Amer. hort. pp. 1294–1296. 1901.

[6] ROSE, J. N., Notes on useful plants of Mexico. Contrib. U.S. Nat. Herb. 5:212. 1899.

countries farther south, which were undoubtedly the original home of the less drought-resistant *P. vulgaris* and *P. lunatus*. I have been unable to secure descriptions of all of the wild species reported from Mexico and Central America, but the specific characters of the greater part of the list has been gone over very carefully.

Phaseolus brevicalyx Micheli (Mém. Soc. Phys. Genève **34**: 261. *pl. 12.* 1903) is a close relative of the tepary. The latter differs from this species, however, in being glabrous or only slightly puberulent, while *P. brevicalyx* is described as pilose. It further differs strongly in the following points: petioles 2–10 cm. long (average 6.8 cm.) rather than 1–3 cm., stipules lanceolate and appressed rather than broadly ovate and spreading, calyx never punctate with black spots.

The description of *P. proriferus* M. E. Jones, though very incomplete, indicates that this also is a near relative of the tepary, but it seems to differ from the tepary in being more robust and in the rhombic-ovate, abruptly acuminate leaflets.

The following description of *P. acutifolius* Gray[7] seems to agree with the tepary in every particular:

> P. ACUTIFOLIUS, sp. nov.—Volubilis; ramis gracillimis puberulis; foliolis subovato-lanceolatis e basi ad apicem usque attenuatis acutis integerrimis scabrido-puberulis; pedunculis paucifloris folio brevioribus, bracteis bracteolisque subulatis minimis deciduis; pedicellis flore aequilongis; calyce profunde bilabiato, labio superiore vix emarginato dentibus lateralibus et infimo ovato-oblongis subaequalibus tubo paulo brevioribus; legumine compresso lato-lineari falcato pubescente; seminibus complanatis leviter rugosis.—Mountain valley 30 miles east of El Paso; Sept.—Plant in general aspect and foliage much resembling a slender narrow-leaved variety of *P. helvolus;* but the leaves are more tapering and pointed; the 2–3-flowered peduncles are shorter than the leaf, and seldom longer than the common petiole; and the pedicellate flowers are smaller than those of *P perennis*. It belongs to the section DREPANOSPRON, having a flat and falcate legume, not much curved, two inches long, a quarter of an inch wide, 8–9-seeded. Seeds oval, compressed, somewhat shining, lightly rugose. The leaflets are from one to two inches long, varying from ovate-lanceolate to lanceolate from a broad base.

Specimens of the tepary have been submitted to Dr. J. N. ROSE, who states in a letter: "I quite agree with you that your Indian

[7] GRAY, ASA, Plantae Wrightianae. pp. 43, 44.

bean is different from *P. vulgaris*, although rather closely related to it. I would suggest that you compare it with *P. acutifolius*." In a later letter he says: "We have specimens named by Dr. GRAY which look very much indeed like your specimen." Unfortunately I have been unable to obtain authentic wild examples of *P. acuti-*

FIG. 6.—*Phaseolus acutifolius* var. *tenuifolius* A. Gray

folius. Several plants occur in the herbarium of the university which bear this label, but they do not at all agree with GRAY'S original description. Photographs of these plants and also pressed specimens of the tepary were submitted to Dr. B. L. ROBINSON of the Gray Herbarium where the type specimen of *P. acutifolius* and several of its varieties are found. The matter was turned over to

Dr. C. A. WEATHERBY, who after careful comparison with the types left by Dr. GRAY wrote as follows:

> The type of *P. acutifolius* Gray is a plant collected by WRIGHT in western Texas in Sept. 1849. . . . . Your plant is evidently near it, differing in its much longer petiolules of the central leaflet and in its broader leaflets. The plants [referring to the photographs] with narrow leaflets are *P. acutifolius* var. *tenuifolius* Gray [fig. 6]. There is also a second variety mentioned by Dr. GRAY in the *Plantae Wrightianae* [2:33] without name, which has leaflets larger and broader than in your plant and of which I will send a tracing.

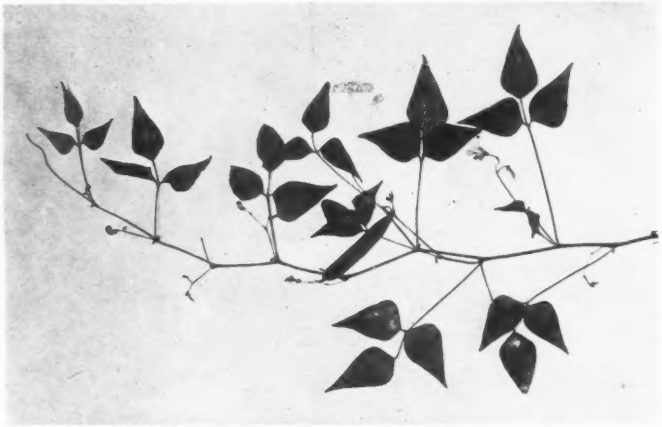


FIG. 7.—The tepary (*Phaseolus acutifolius* var. *latifolius*, n. var.)

The tracing of the type specimen of *P. acutifolius* Gray furnished by Dr. ROBINSON was found on comparison to be intermediate in form between *P. acutifolius* var. *tenuifolius* on the one extreme and the tepary on the other. The tracing of Dr. GRAY's larger, broader-leaved, unnamed variety of *P. acutifolius*, although larger than the small specimen of the tepary which I submitted to Dr. ROBINSON, was identical with the tepary as grown upon the testing grounds at this station. In fact, this tracing might have been drawn from any one of a number of herbarium specimens of the tepary which I have made during the present season (figs. 7–9).

Careful measurements of the leaves of the specimen of *P. acutifolius* found in the National Herbarium were furnished by

No. 4
Phaseolus acutifolius n. sp.
Collected in Expedition from Western Texas to El Paso
New Mexico, May—October 1848, by Charles Wright
Phas.
Legumen glaud. falcata

FIG. 8.—*Phaseolus acutifolius* A. Gray: from tracing of the type specimen made for the writer under the direction of Dr. B. L. ROBINSON, Gray Herbarium.

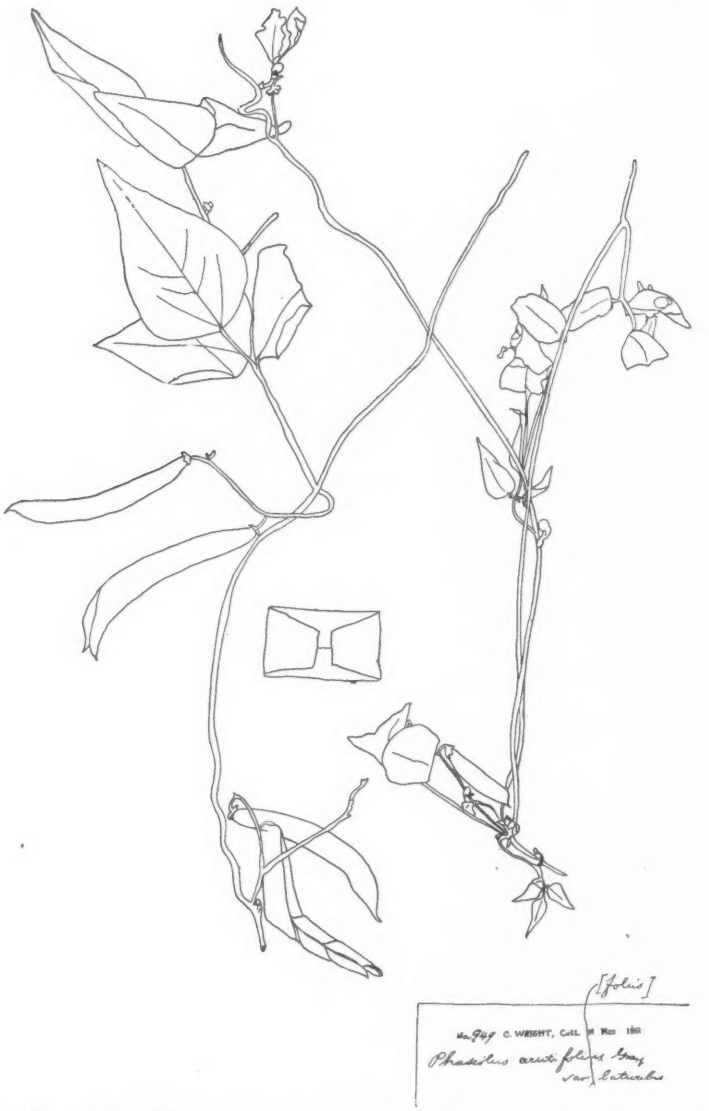


FIG. 9.—*Phaseolus acutifolius* var.: from tracing of Dr. GRAY's unnamed variety collected by WRIGHT in a valley of Sonora; tracing made for the writer under the direction of Dr. B. L. ROBINSON, Gray Herbarium.

Professor J. J. THORNBER. In the following table these are compared with similar measurements of the tepary and the tracing of the broad-leaved variety furnished by Dr. ROBINSON. The measurements of the tepary were made from 100 mature leaves, taken at random from some 30 varietal plots during August 1911.

TABLE IV

	Phaseolus acutifolius	Tepary	GRAY'S unnamed variety
Length terminal leaflet	40–46 mm.	40–95 (av. 64) mm.	56–71 mm.
Width terminal leaflet	16–21	22–52 (av. 37)	22–41
Length lateral leaflet	30–42	38–78 (av. 56)	42–52
Width lateral leaflet	12–23	20–50 (av. 33)	23–38
Length terminal petiolule	8–13	16–34 (av. 22)	11–18
Length petioles	30–40	20–100 (av. 68)	25–46

It may now be noted that the tepary leaves are decidedly larger and broader than those of the type of *P. acutifolius*, and that in the length of the petiolule of the terminal leaflet they far exceed the specific type. In most of these characters, moreover, they exceed the measurements of GRAY'S unnamed variety. It must be remembered, however, that of this latter there is but one specimen, and that upon it there is only one well matured leaf whose measurements are the maximum given. In view of the above careful comparisons but one conclusion seems possible. The tepary and GRAY'S unnamed broad-leaved variety are identical. Thus, in their broad leaves and robust growth they exhibit the opposite extreme of variation from the type of *P. acutifolius* that *P. acutifolius* var. *tenuifolius* does in the direction of narrow leaves and slender habit. GRAY'S mention of this broad-leaved variety is as follows:

> P. ACUTIFOLIUS; var. foliolis majoribus ovatis acuminatis, legumine majo.e (3-pollicari).—Valleys of Sonora, Sept. (949).—Plantae Wrightianae (2:33).

Although GRAY recognized it as a distinct variety, his failure to give it a name and more careful description is probably due to the fact that he had only one specimen. This lack of material I am now able to supply. I feel, therefore, that I am safe in adding to the species of *Phaseolus* which are used as esculents the name of

the tepary (*P. acutifolius* A. Gray), and suggest that this variety be called *P. acutifolius* var. *latifolius*. The description is as follows:

PHASEOLUS ACUTIFOLIUS A. Gray var. **latifolius,** var. nov.—Tepary.—Annual: stems recumbent, spreading or twining, 0.5–3 m. long, glabrous to puberulent: leaves smooth above, with prominent veins beneath, glabrous throughout or slightly puberulent beneath; stipules lanceolate, 2 mm. long, 1 mm. broad, striate, appressed; petioles slender, 2–10 cm. long (av. 6.8 cm.); leaflets stipellate; terminal leaflet stalked, large, 4–9.5 cm. long (av. 6.4 cm.), 2.2–5.2 cm. wide (av. 3.7 cm.), average ratio length to width 1.74, ovate to broadly lanceolate, gradually narrowed and acute at apex; petiolule of terminal leaflets 1.6–3.4 cm. long (av. 2.2 cm.); lateral leaflets same general shape as terminal leaflet but slightly smaller and inequilateral, 3.8–7.8 cm. long (av. 5.6 cm.), 2–5 cm. broad (av. 3.3 cm.): inflorescence axillary; bracts and bractlets small, deciduous: flowers medium sized, pedicellate, white or pale violet: calyx short, 3–4 mm. long, broadly campanulate, 4-toothed (upper two lobes uniting into one), teeth acuminate, pubescence on teeth and calyx scattered and fragile: banner broad, emarginate, in flower more than half reflexed, biauriculate at base, 8–10 mm. long; wings exceeding banner, obovate to spatulate, 10–15 mm. long, auriculate on one side; keel narrow, two or three turns to the spiral: stamens in two sets (9 and 1): legume 2–7-seeded (average 4.9), 5–9 cm. long (av. 7.3 cm.), 8–13 mm. wide (av. 10.5 mm.), ciliate when young, puberulent, slightly pubescent, or smooth when mature, straight or slightly curved: seeds of different varieties white, yellow, brown, or bluish black to deep violet, either self-colored or variously flecked (no red-seeded varieties have yet been observed), round oval to nearly round (as the navy bean) to strongly flattened (like a diminutive lima).—Fig. 10.

The following table gives the averages of size and shape of the seeds as determined by measurement of at least 25 normal specimens of each of 48 different strains.

TABLE V

	Length mm.	Width mm.	Thickness mm.	Ratio $\frac{L.}{W.}$	Ratio $\frac{W.}{T.}$
Maximum varietal average . . .	9.78	6.68	4.76	1.80	2.10
Minimum varietal average. . . .	6.93	3.88	2.66	1.32	1.20
Average for all varieties.	8.56	5.68	3.80	1.49	1.51

COULTER[8] gives as the habitat of *P. acutifolius* "mountain valleys west of the Pecos, and in adjacent New Mexico and Mexico."

[8] COULTER, J. M., Botany of western Texas. Contrib. Nat. Herb. **2**:89. 1894.

I do not know of authentic specimens of *P. acutifolius* or its broad-leaved variety being recorded from Arizona,[9] but I have little doubt that a close search of the canyons of the southern part of the state will reveal its presence. The tepary is grown by the Indians and Spanish settlers throughout southern Arizona and northern Sonora. The further limit of its cultivation is not known to me, but it probably extends from southwest Texas, across New Mexico, Arizona, California, southward into northern Mexico.

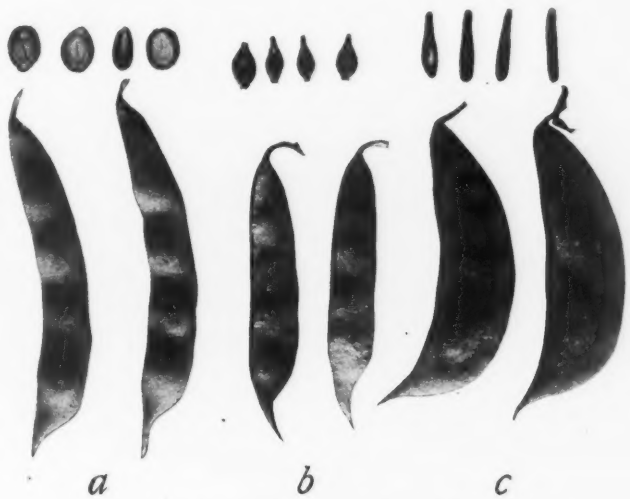


FIG. 10.—Pods of bean (*a*), tepary (*b*), and lima bean (*c*)

In order to discover whether the tepary has yet found its way into the hands of the commercial seedsmen, a list of the leading seedsmen of the country was secured. Especial attention was paid to making this list as complete as possible with regard to the seedsmen of the Southwest. Catalogues were then secured, and at least one sample of every named variety was ordered. Wherever from the description, or lack of description, there appeared a

[9] It has already been mentioned that the four Arizona specimens in the herbarium of the university, which were labeled *P. acutifolius* Gray, are *P. acutifolius* var. *tenuifolius* Gray.

possibility that the variety in question might be closely related to the tepary, it was ordered from every available source. In this manner 216 more or less distinct varieties were secured. Nothwithstanding the fact that anyone familiar with the tepary could tell at a glance that none of these belonged to this group, all of those varieties which in any way resembled it were planted. In the seedling stage further confirmation of their relationship to *P. vulgaris* was made unnecessary by the uniformly long petioles of the first pair of aerial leaves.

Varieties

Domesticated from the neighboring canyons and cultivated in small patches, attended at best by a crude husbandry, and dependent upon the precarious summer rains and uncertain floods from the mountain washes for irrigation, the tepary has lost none of its native hardiness. Like other cultivated plants, however, it has responded to domestication in the production of a number of more or less distinct varieties. These varieties manifest themselves chiefly in the color of the flowers and in the shape and color of the seed. The habit of growth, foliage, and pod characters show but little change, with the exception that the white-seeded sorts seem to have slightly smaller leaves than do those with yellow or darker colored seeds.

Food value of the tepary

There is considerable difference of opinion as to the relative palatability of beans and teparies. Among the Indians and Mexicans the pink bean is preferred to the tepary, as they say it has a better flavor. These people, however, make the same difference between the pink bean and the white navy beans which are shipped in from the East.

Teparies should be soaked 12 hours before cooking, during which time they swell to at least twice their original volume and more than double in weight. In this respect they markedly surpass the bean. The greater swelling and absorptive power of the tepary is probably due to its greater initial specific gravity, which is about 1.33 as compared with 1.22 for the bean. After

soaking and cooking thoroughly, the tepary is no more dense or heavy than the bean, having overcome this in its greater expansion.

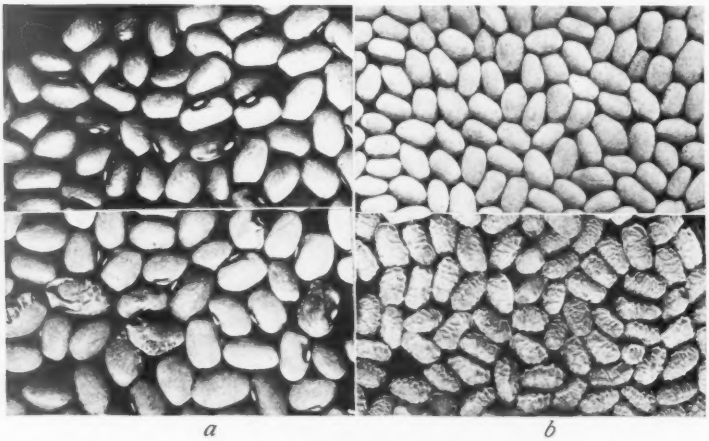
A gentleman well acquainted with the customs of the Mexican and Indian users of the teparies states that these legumes are preferred to the bean and are highly prized for the preparation of light soups. At first I thought this might be due to the extraction of less solid matter, resulting in a thinner, more delicate soup. An experiment, however, was carried out whereby an equal dry weight of beans and teparies were boiled until well done. The liquors were then made up to equal volumes, well shaken, and 100 cc. of each evaporated to dryness. Contrary to expectation, the dry residue was greater for the teparies than for the beans. The residue from the teparies was much clearer, more gelatinous, and dried into a translucent, horny flake; whereas that from the beans was more friable, and dried into a somewhat brittle mass.

Under the husbandry of the Indians, this group has shown great variation. I have been able to segregate and grow more than 40 distinct agricultural varieties and I do not doubt that many more exist which I have not yet secured. In productivity, especially where the conditions are adverse, the tepary far exceeds the bean. In 9 experiments covering three years' work at Yuma, two at Tucson, and three at McNeal, the average yield of the tepary varieties has been slightly in excess of four times the average for the varieties of the kidney bean. The explanation of these greater yields on the part of the teparies, in all probability, lies in the perfect physiological adaptation of these native plants to the climatological environment in which they had their development both as wild and domesticated species. As examples of this perfect adaptation may be mentioned the following:

a) Ability to germinate quickly in the presence of a low moisture content of the soil. This enables them to take advantage of the sudden desert downpours which wet the ground and then rapidly disappear by evaporation. Teparies, which are able to germinate and come up in 3–5 days' less time than the bean, are thus able to get their leaves into the air and their roots into the soil by the aid of showers which would be wholly inadequate for securing a stand of a less specialized crop.

When tepary seeds are placed in moist soil and the soil is pressed snugly about them, they will take up enough moisture to cause the skins to wrinkle within 5 minutes. When thrown in water, they will wrinkle within 3 minutes to a condition such as is assumed by the skin of the kidney bean only after 3–6 hours of soaking (fig. 11).

b) When once the tepary has established itself in the soil, it is able to withstand protracted seasons of water famine without permanent injury. The ability to recover from the effects of



a *b*

FIG. 11.—Above, beans dry (*a*) and teparies dry (*b*); below, beans after soaking in water 45 minutes (*a*) and teparies after soaking in water 3 minutes (*b*).

drought is not possessed by beans to a marked degree. This places them at a great disadvantage in a competition with the tepary under such conditions as are frequently met in the practice of dry farming.

c) The tepary is inured to the greatest extremes of our summer temperatures and will bloom and set seed during any month from May to November. On the other hand, when the blooming period of beans happens to fall within the season of extreme heat, the buds will for the most part either abort before blooming or else the flowers will fall without setting pods. For these reasons the tepary is a

more sure and dependable crop, often giving fair returns when beans are a total failure (fig. 1). As a dry land crop in the south-central plains and Rocky Mountain regions the tepary will in the near future in all probability find a place of considerable economic importance.

ARIZONA AGRICULTURAL EXPERIMENT STATION
TUCSON, ARIZONA

A COMPARISON OF THE AMERICAN BROWN-ROT FUNGUS WITH SCLEROTINIA FRUCTIGENA AND S. CINEREA OF EUROPE

W. A. MATHENY

(WITH SIX FIGURES)

Is the American brown-rot fungus (*Sclerotinia fructigena*) of stone fruits identical with the fungus bearing the same name and occurring throughout Europe, but there found exclusively upon pome fruits? That *S. fructigena* should occur in Europe only on pome fruits and in this country only on stone fruits appears unusual and to many improbable. If *S. cinerea* is the fungus attacking stone fruits in Europe, as all the European writers maintain, then the suggestion seems pertinent that our brown rot of stone fruits is caused by the same fungus. In fact, ADERHOLD and RUHLAND (**5**) assert that our species is *S. cinerea*. They came to this conclusion after an examination of a few preserved apothecia sent them by NORTON, and in the absence of a more extended study their evidence appears inconclusive.

At the suggestion of Professor C. F. HODGE of Clark University, the writer has undertaken a comparative study of these two species. At first it was intended merely as a study in variation, but it soon of necessity became a problem in taxonomy. Our final interest was to determine as nearly as possible which one of the above species agrees more nearly with the rot of our stone fruits.

Historical sketch

The history of *Sclerotinia fructigena* dates back to 1796, when PERSOON (**17**) gave the name *Torula fructigena* to a fungus which he found on the decayed fruit of *Prunus domestica*, *Amygdalus persica*, and *Pyrus*. This same name was retained by other writers, notably FUCKEL (**12**), ALBERTINI and SCHWEINIZ (**6**), SACCARDO (**23**), and RABENHORST (**21**). In 1801 PERSOON (**18**) changed it to *Monilia fructigena*, a name by which it is generally

known today. KUNZE and SCHMIDT (**14**) a little later referred it to *Oidium fructigenum*, under which name it received attention from many writers, among the first of whom should be mentioned EHRENBERG (**10**), COOKE (**8**), DUBY (**9**), and FRIES (**11**). In 1822 PERSOON (**19**) renamed this fungus *Acrosporium fructigenum*, a classification which was never accepted by other writers. WALLROTHIO (**29**) placed it in the genus *Oospora*, calling it both *O. candida* and *O. fructigena*, while VON THÜMEN (**27**) first classed it as *Oidium Wallrothii*, but later (**28**) changed it to *O. fructigenum*. The first writers to attach any economic importance to this fungus were VON THÜMEN (**28**) and HALLIER (**13**). SCHRÖTER (**25**) in 1893, being confident of its ascomycetous nature, placed it in the genus *Sclerotinia*. This classification was confirmed in Europe in 1904 by ADERHOLD (**1**). NORTON (**16**) had first discovered apothecia in 1902.

Sclerotinia cinerea was first described as *Monilia cinerea* by BONORDEN (**7**) in 1851. He noted it forming small, gray, sometimes brownish conidial tufts on fruit. This species has many times been confused with *S. fructigena*, in fact many of the descriptions given the one could apply equally well to the other. SACCARDO (**23**) in 1886 recognized *Monilia cinerea*, while SCHRÖTER transferred it to the genus *Sclerotinia* along with *M. fructigena*. WORONIN (**30**) in his excellent study published in 1900 established beyond a doubt the fact that the species are distinct. This opinion is held by SORAUER (**26**).

Difference between S. fructigena and S. cinerea

Several points of difference between these two species have been cited by ADERHOLD (**2, 3, 4**), WORONIN (**30**), and others. Of these, the most striking are as follows:

1. The conidia of *S. fructigena* are always larger than those of *S. cinerea*.

2. There is a difference in shape of the conidia, those of the former having an elongated ellipsoidal form, while those of the latter are more rounded.

3. The conidial tufts of *S. fructigena* are light brownish-yellow or ocher and are always large, while those of *S. cinerea* are ash-gray

and always small. It is noted that the conidial tufts of the former often grow together, exhibiting a smooth upper surface. This does not occur with the latter species.

4. *S. fructigena* occurs on pome fruits, while *S. cinerea* occurs on stone fruits.

5. The ascospores of *S. fructigena* are sharply pointed at the ends, while those of *S. cinerea* are rounded on the ends. The former are without oil droplets, the latter possess them.

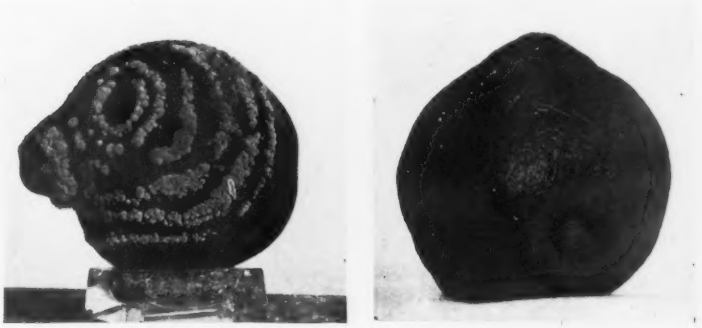
Observations

Our observations in this study are limited to behavior on fruit and in pure culture, size of conidia, and size of asci and ascospores. No apothecia could be obtained from Europe; however, the measurements made by ADERHOLD and RUHLAND were available.

In the beginning, letters requesting pure cultures or mummied fruits bearing both species were sent to different parts of Europe. Pure cultures of *S. cinerea* and *S. fructigena* were twice sent me by Dr. J. WESTERDIJK of the Association internationale des botanistes, Bureau pour la distribution de cultures de moisissures, Amsterdam. Mummied fruits bearing *S. fructigena* were sent me by the following persons: Dr. LUIGI MONTEMARTINI of the University of Pavia; Professor Dr. C. WEHMER of Hannover; Professor Dr. PAUL SORAUER of Berlin; GY DE ISTVANFFI of Budapest; and Professor Dr. G. LUSTNER of Geisenheim. Similar fruits were also obtained from the government experiment stations at Geisenheim and Dahlem. I also received a box of mummied fruits from the Department of Agriculture of New South Wales.

Among the fruits sent me by Dr. LUSTNER were some mummied plums bearing *Sclerotinia cinerea*. Its outward appearance was so strikingly different from that of *S. fructigena* that its recognition was a matter of first glance. Both species were easily isolated on other fruits and then in pure cultures. This plan gave an easy and practical method of observing the forms as they grew side by side, many times on the same pear or apple and oftentimes in the same petri dish.

BEHAVIOR ON FRUIT.—Quinces taken from the same tree, and subjected to the same external conditions, were inoculated with



A *B*

FIG. 1.—*A*, quince bearing the European *S. fructigena;* conidia taken from a mummied fruit obtained from Dr. P. SORAUER of Berlin; *B*, quince taken from the same tree as *A*, but inoculated with local *Sclerotinia* spores; quinces inoculated with the European *S. cinerea* behaved in a similar way.

FIG. 2.—*S. fructigena* on a pear; inoculated from a fruit obtained from Dr. C. WEHMER of Hannover.

conidia of *S. fructigena* and of *S. cinerea* which were sent from Europe, and with conidia from *Sclerotinia*-infected plums growing in Worcester. The growth of *S. fructigena* was very slow, however, producing in two weeks large, yellowish conidial tufts which arrange themselves in rings (fig. 1, *A*). The quinces inoculated with *S. cinerea* and the local *Sclerotinia* behaved in exactly the same way, both turning the fruit brown but producing no conidia. In different varieties of apples, 25 experiments gave exactly similar

FIG. 3.—*A*, *S. fructigena* on a pear; inoculated from fruit obtained from Dr. LUIGI MONTEMARTINI of Pavia; *B*, local *Sclerotinia* on a pear exactly similar to *A*; this pear was inoculated 10 days after *A*, and both photographed the same day, 13 days after the inoculation of *A*.

results as those obtained with the quinces, that is, large, yellowish conidial tufts from the *S. fructigena*, and no conidia at all from the *S. cinerea* and the local *Sclerotinia*. If the apples were cut in quarters, and the conidia placed directly on the exposed flesh of the fruit, an abundant growth of spores was obtained. Quartered apples inoculated in this manner with the spores of *S. fructigena* always gave large, yellowish tufts of conidia. When *S. cinerea* was used, the conidia appeared in small ash-gray tufts entirely unlike those of *S. fructigena*. The local *Sclerotinia* spores produce

conidia a little sooner than those of *S. cinerea*, but in other respects their resemblance is very close.

On pears, 100 experiments were tried. With the *S. fructigena* inoculations the results were uniformly the same as on the quince and apple. The growth was much slower than that of the local *Sclerotinia* on similar fruit, but the usual large, yellowish conidial tufts were produced (fig. 2).

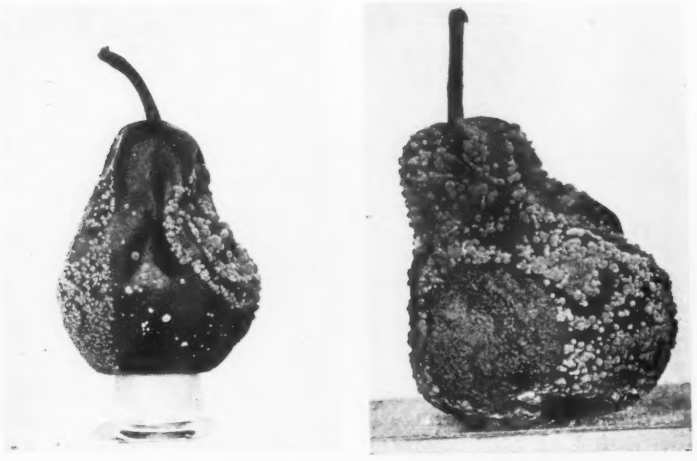
The European *S. fructigena* and the local *Sclerotinia* were grown many times on the same pear (figs. 3 and 4), and the results were no different from those obtained when they were grown separately.

BEHAVIOR IN PURE CULTURE.—Pure cultures of the European *Sclerotinia fructigena* and of the local brown-rot fungus have been grown side by side during the past year (fig. 5). Hundreds of cultures of each have been maintained on various media: plum agar, bread agar, beet decoction, apple gelatin, etc. It was thought that should these fungi be identical, a similarity in cultural growth might appear in some of these media. No evidence of any such similarity has so far been observed. Cultural characteristics of each are as distinctly different today as they were one year ago when this experiment was started.

Comparison of the conidia of S. fructigena, S. cinerea, and local Sclerotinia

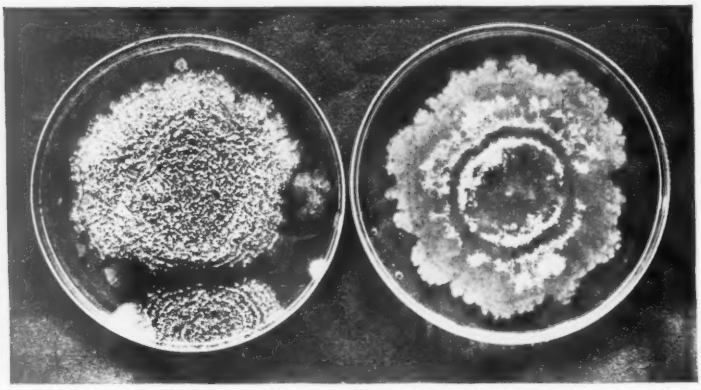
In the accompanying table are arranged the comparative sizes of the conidia of *S. fructigena* and *S. cinerea* as they have been given by different writers.

AUTHOR	CONIDIA	
	S. fructigena	*S. cinerea*
Saccardo (**23**)	25×10–12	15–17×10–12
Lindau (**15**)	20–24×12–14	12–13×9–10
Woronin	20.9 ×12.1 to 24.5 ×13.2	12.1 × 8.8 to 13.2 × 9.9
Schröter	18–24×10–12	15–18×10–12
Aderhold and Ruhland	25×13	13.8 × 9.9



A *B*

FIG. 4.—*A*, local *Sclerotinia* and European *S. fructigena* on the same pear; *B*, local *Sclerotinia* on a pear surrounded by *S. fructigena* taken from fruit sent by Dr. GY DE ISTVANFFI of Budapest.



A *B*

FIG. 5.—*A*, local *Sclerotinia* from plums on 1 per cent sugar, 1 per cent malic acid, and 6 per cent gelatin medium; *B*, *S. fructigena* from Europe on the same medium; both plates had the same external conditions; in both plates the gelatin is liquefied in *B* sooner and to a greater extent.

Before attempting to give the size of the conidia of the American brown-rot fungus, it was considered necessary to make a series of comprehensive measurements of the spores taken from fruit from different parts of the country. Such measurements were made. The method of this work was that of the ordinary laboratory procedure. An ocular micrometer having a scale value of 3.6 μ was used. Unconscious selection was avoided by measuring all the spores that arranged themselves in bunches on the slide, or always measuring the one nearest the right side of the eyepiece scale. Care was taken to allow the spores to become fully turgid in the water before the measurements were started.

The results obtained in these measurements are of considerable interest from another point of view. WORONIN and POLLOCK (20) have suggested that these conidia vary in size to a considerable degree according to the host or culture. Others suggest that light and darkness also cause a variation in size. In none of these instances, however, is the method of measurement mentioned or the number of conidia measured. In the results obtained in this study no such variation was ever in evidence. On the other hand, when all the measurements were done and the figures computed for a mean, variation in size of conidia was found to be practically nothing.

SPORE MEASUREMENTS

(In each case the upper row of figures represent microns, and the lower row the number of spores of that size.)

SPORES FROM MUMMIED PLUMS SENT BY J. W. ADAMS, FRANKLIN, IND.

No. spores measured	Length										Mean
	11.5	12.2	13	13.7	14.4	15.1	15.8	16.6	17.2	18	14.4 μ
	3	4	13	20	50	27	19	6	1	2	
145	Width										
	7.2	7.9	8.6	9.4	10.2	10.8	11.5	12.2	.....	.....	9.4 μ
	4	23	31	47	19	11	7	3	.....	.....	

SPORES FROM MUMMIED PLUMS SENT BY F. K. HACKETT, LACONIA, N.H.

No. spores measured	Length											Mean
	13 4	13.7 7	14.4 12	15.1 31	15.8 14	16.6 14	17.2 7	18 13	18.7 3	19.4 1	20.1 1	15.1 μ
107	Width											
	8.6 8	9.4 8	10.2 21	10.8 34	11.5 23	12.2 11	13 2	....	....	....	....	10.8 μ

SPORES FROM MUMMIED APRICOTS SENT BY E. H. SMITH, BERKELEY, CAL.

No. spores measured	Length											Mean
	12.2 2	13 7	13.7 12	14.4 26	15.1 30	15.8 21	16.6 15	17.2 11	18 7	18.7 5	19.4 6	20.1 4	15.1 μ
146	Width												
	8.6 12	9.4 11	10.2 29	10.8 43	11.5 26	12.2 15	13 5	14.4 3	15.1 2	....	....	....	10.8 μ

LOCAL SCLEROTINIA ON CHERRIES

No. spores measured	Length											Mean
	11.5 2	12.2 7	13 13	13.7 15	14.4 28	15.1 36	15.8 14	16.6 6	17.2 6	18 5	19.4 1	15.1 μ
133	Width											
	7.9 17	8.6 34	9.4 34	10.2 28	10.8 14	11.5 3	12.2 3	....	....	....	....	9 μ

LOCAL SCLEROTINIA ON APRICOT

No. spores measured	Length											Mean
	11.5 2	12.2 11	13 18	13.7 27	14.4 41	15.1 21	15.8 17	16.6 4	17.2 8	18 2	18.7 3	14.4 μ
166	Width											
	7.2 4	7.9 11	8.6 37	9.4 49	10.2 28	10.8 14	11.5 16	12.2 7	....	....	....	9.4 μ

LOCAL SCLEROTINIA ON BALDWIN APPLE

No. spores measured	Length												Mean
	12.2	13	13.7	14.4	15.1	15.8	16.6	17.2	18	18.7	19.4	20.1	14.4 μ
	5	14	41	62	32	21	13	17	16	13	9	2	
245	Width												
	7.9	8.6	9.4	10.2	10.8	11.5	12.2	13	....	....	....	....	10.2 μ
	11	24	41	62	42	39	17	9	....	....	....	....	

CONIDIA OF *S. fructigena*, FROM FRUIT SENT BY DR. GY DE ISTVANFFI, BUDAPEST

No. spores measured	Length										Mean
	18	18.7	19.4	20.2	20.8	21.6	22.3	23	23.7	24.4	21.6 μ
	14	21	27	30	35	49	13	6	4	2	
201	Width										
	8.6	9.4	10.2	10.8	11.5	12.2	13	13.7	14.4	.....	10.8 μ
	7	18	50	62	31	19	8	3	3	.....	

CONIDIA OF *S. fructigena*, FROM AN AMERICAN QUINCE WHICH HAD BEEN INOCULATED WITH CONIDIA SENT BY THE GOVERNMENT EXPERIMENT STATION AT DAHLEM (BERLIN)

No. spores measured	Length													Mean
	....	17.2	18	18.7	19.4	20.2	20.8	21.6	22.3	23	23.7	24.4	25.1	25.8	21.6 μ
	1	4	16	7	18	22	23	64	24	12	5	3	2	1	
202	Width														
	8.6	9.4	10.2	10.8	11.5	12.2	13	13.7	14.4	15.1	15.8	16.6	....	....	10.8 μ
	10	11	19	67	21	25	15	19	11	1	2	1	....	....	

CONIDIA OF *S. fructigena*, ON A PEAR

No. spores measured	Length														Mean
	18	18.7	19.4	20.2	20.8	21.6	22.3	23	23.7	24.4	25.1	25.8	26.5	27.2	27.9	22.3 μ
	4	4	10	16	24	47	82	28	22	21	25	10	5	2	3	
303	Width															
	10.2	10.8	11.5	12.2	13	13.7	14.4	15.1	15.8	16.6	17.2	18	....	....	....	21.2 μ
	1	12	49	61	48	45	46	32	4	3	1	1	....	....	....	

CONIDIA OF *S. cinerea*, FROM FRUIT SENT BY DR. G. LUSTNER, GEISENHEIM

No. spores measured	Length										Mean
	11.5	12.2	13	13.7	14.4	15.1	15.8	16.6	17.2	18	14.4 μ
	4	15	24	30	44	34	18	5	5	2	
181	Width										
	8.6	9.4	10.2	10.8	11.5	12.2	13	13.7	14.4	....	10.8 μ
	7	14	31	49	24	25	13	9	9	....	

Number of American brown-rot conidia measured, 942; average size, 14.7×9.9 μ.
Number of conidia of *S. cinerea* measured, 181; average size, 14.4×10.8 μ.
Number of conidia of *S. fructigena* measured, 665; average size, 22.1×11.2 μ.

Asci and ascospores

Some attention has been given to the size of the asci and ascospores of *Sclerotinia fructigena* and *S. cinerea*. In the accompanying table are given the different measurements that have been made.

AUTHOR	*S. fructigena*		*S. cinerea*	
	Asci	Ascospore	Asci	Ascospore
Aderhold and Ruhland	120–180 × 9–12	11–12.5 × 5.6–6.8	89.3–107.6 × 5.9–6.8	6.2–9.3 × 3.1–4.6
Reade (22)	125–215 × 7–10	10–15 × 5–8	.....	.....
Pollock (20)	130–179 × 9.2–11.5	11.4–14.4 × 5–7	.....	.....

The following explanation should be given of the above measurements. The asci and ascospores of *S. fructigena* measured by ADERHOLD and RUHLAND were obtained from mummied apples in their experiments at Dahlem. Their *S. cinerea* material was the preserved material sent them by NORTON. The measurements made by READE were of fresh material sent him by NORTON. POLLOCK's measurements were of fresh material obtained in Michigan.

In order to determine what variation in size of asci and ascospores occurs in this country, a series of measurements was made of fresh material from different states. The measurements were made in the usual way. In each instance 100 ascospores and 70 asci were measured. From the resulting figures the following table is arranged.

MEASUREMENTS OF ASCI AND ASCOSPORES

Apothecia from	Host	Asci	Ascospores
New Haven, Conn.	Peach	144–188×6.8–10.8 Mostly 162×8.6	10.8–14.4×4.3–7.6 Mostly 12.6×5.4
Grafton, Mass.	Peach	136–202×7.5–11 Mostly 169×9.4	11.5–14×5–7.2 Mostly 12×5.4
Grafton, Mass.	Plum	144–162×7.2–10.8 Mostly 151×9.3	10–14×5–7.6 Mostly 12.2×6.1
West Boylston, Mass.	Peach	133–187×6.8–10 Mostly 158×8.2	10.8–15.1×5.4–7.2 Mostly 12.9×6.1
College Park, Md.	Peach	129–194×7.2–10.8 Mostly 162×9.3	8.6–15.1×5.7–7.9 Mostly 12.2×6.4
College Park, Md.	Plum	126–183×6.5–10.8 Mostly 151×9.6	8.6–14.4×5–7.2 Mostly 11.5×6.4
Madison, Wis.	Peach	137–190×6.5–10.8 Mostly 165×9.3	10.8–15.1×5–7.2 Mostly 13.1×6.5
Geneva, New York	Peach	133–176×6.5–9.4 Mostly 160×8.4	11.5–14.4×5.7–8 Mostly 12.8×6.2
Lafayette, Ind.	Peach	135–192×7.2–11.1 Mostly 166×8.8	9.4–13.7×5.6–7.9 Mostly 12.2×6

GENERAL AVERAGE OF THE ABOVE MEASUREMENTS

Host	Asci	Ascospores
Peach	135–190×6.9–10.5 Mostly 163×8.9	10.5–14.5×5.2–7.5 Mostly 12.5×6
Plum	135–173×6.8–10.8 Mostly 151×9.4	9.3–14.2×5–7.4 Mostly 11.8×6.3

It is seen that the results here obtained correspond closely with the measurements given by POLLOCK and READE, indicating that the same species was considered in all three cases. It is further noted that these measurements correspond with those given by ADERHOLD and RUHLAND for the European *S. fructigena* and are very little larger than those given by them for their *S. laxa* which they obtained from apricots. It is to be remembered that in the case of both these species very few measurements have been

made, and that a more comprehensive study may reveal a wider variation than is here indicated.

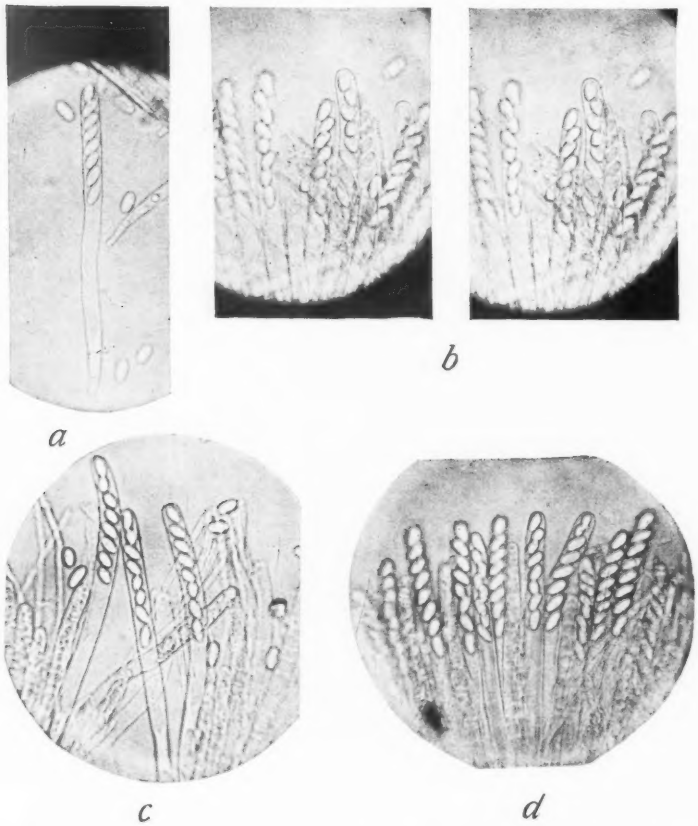


FIG. 6.—Asci and ascospores: *a*, ascus from Maryland plum; *b* and *c*, asci and ascospores from Maryland plums; *d*, from Maryland peach; all ×400.

Conclusions

The 300 experiments on different fruits show in every instance a wide difference between the *S. fructigena* of Europe and the local brown rot. First, they differ in the rate of growth, the former

being much slower than the latter (fig. 3). Second, the conidial tufts do not agree in size, shape, or color. The *S. cinerea* when grown on plums, pears, apples, and quinces agrees in practically every instance with the local *Sclerotinia*.

When grown in pure culture, the European *S. fructigena* never agreed with the local form (fig. 5); 300 cultures of each were made. The conidia of the former are larger than those of the latter. Those of the latter, however, agree in size with the conidia of *S. cinerea*.

While the asci and ascospores of the European *S. fructigena* and the American form apparently correspond in size, there are differences that remain distinct. The ascospores of the former are sharply pointed at each end and are free from oil droplets, while the ascospores of the latter are rounded at the ends and possess oil droplets (fig. 6). No exception was found to this rule.

The American brown rot of stone fruits is not identical with *S. fructigena* occurring in Europe on pome fruits. It agrees more nearly with *S. cinerea* and should be referred to that species.

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LITERATURE CITED

1. ADERHOLD, R., Über eine vermuthliche zu *Monilia fructigena* Pers. gehörige *Sclerotinia*. Ber. Deutsch. Bot. Gesells. **22**: 262–266. 1904.
2. ———, Die *Monilia* (*Sclerotinia*)-Krankheiten unserer Obstbäume und ihre Bekämpfung. Kaiserl. Biol. Anst. Land und Forst. Flugblatt. no. 14. 1908.
3. ———, Über die in den letzten Jahren in Schlesien besonders hervorgetretenen Schäden und Krankheiten unserer Obstbäume und ihre Beziehungen zum Wetter. Bot. Abt. Versuchs. Königl. Pomolog. Instituts zu Proskau. December 1897.
4. ———, Zur *Monilia*-Epidemie der Kirschbäume. Gartenflora. pp. 429–433. 1897.
5. ADERHOLD, R., and RUHLAND, W., Zur Kenntnis der Obstbäum-Sklerotinien. Arbeit. Biol. Abt. Land und Forst. Kaiserl. Gesundheitsamte **4**: 427–442. *pl. 7*. 1905.
6. ALBERTINI, I. B. DE, and SCHWEINIZ, L. D. DE, Conspectus Fungorum in Lusatiae superioris Agro Niskiensi Crescentium. No. 1090. 365. Lipsiae. 1805.

7. BONORDEN, H. F., Handbuch der allgemeinen Mykologie. p. 76. *fig.* 78. Stuttgart. 1851.
8. COOKE, M. C., Handbook of British Fungi **2**:604. 1871.
9. DUBY, J. E., Botanicon Gallicum. Pt. II. 932. Paris. 1830.
10. EHRENBERG, C. G., Sylvae mycologicae berolinenses. Berlin. 1818.
11. FRIES, E., Systema Mycologicum **3**:430. Gryphiswaldae. 1829.
12. FUCKEL, L., Symbolae Mycologicae. p. 348. Wiesbaden. 1869.
13. HALLIER, E., Eine Pilzkrankheit des Steinobstes. Wiener-Obst und Gartenztg. pp. 1272. 1876.
14. KUNZE, G., and SCHMIDT, J. C., Mykologische Hefte **1**:80. 1817.
15. LINDAU, G., in RABENHORST'S Kryptogamen-Flora 1^8:52. 1907.
16. NORTON, J. B. S., *Sclerotinia fructigena*. Trans. Acad. Sci. St. Louis **12**:91–97. *pls. 18–21*. 1902.
17. PERSOON, C. H., Observationes Mycologicae. p. 26. Lipsiae. 1796.
18. ———, Synopsis Methodica Fungorum. p. 693. Gottingae. 1801.
19. ———, Mycologie Europaea. p. 24. Erlangae. 1822.
20. POLLOCK, J. B., Notes on plant pathology. 11th Rep. Mich. Acad. Sci. pp. 51–54. 1908.
21. RABENHORST, L., Deutschlands Kryptogamen-Flora. p. 37. Leipzig. 1844–1853.
22. READE, J. M., Preliminary notes on some species of *Sclerotinia*. Annales Mycol. **6**:109–115. 1908.
23. SACCARDO, P. A., Mycologiae Venetae specimen. p. 177. Patavii. 1873.
24. ———, Sylloge Fungorum **4**:34. 1886.
25. SCHRÖTER, C., Kryptogamen Flora von Schlesien **3**: Pilze. p. 67.
26. SORAUER, P., Handbuch der Pflanzenkrankheiten **2**:288–291. 1908.
27. THÜMEN, F. VON, Der Grind oder Schimmel des Obstes, *Oidium fructigenum*. Oessterr. Landw. Wochenblatt **41**:484. 1875.
28. ———, Fungi Pomicoli. Wien. 1879.
29. WALLROTHIO, F. G., Flora Cryptogamica Germaniae. p. 182. Norimbergae, 1833.
30. WORONIN, M., Über *Sclerotinia cinerea* und *Sclerotinia fructigena*. Mém. Acad. Imp. Sci. St. Pétersbourg VIII. Phys.-Math. Cl. **10**:1–38. *pls. 1–6*. 1899.

OSMOTIC PRESSURE IN POTATOES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 177

M. A. BRANNON

(WITH FOUR FIGURES)

During recent years the problems of periodicity, dormancy, and after-ripening have been investigated by numerous plant physiologists. Among the numerous questions involved, that of osmotic pressure has a prominent place. Naturally, the study of osmotic pressure in living cells affords a difficult and intricate field of research provided the direct method of measurement is employed. If an indirect method, such as the cryoscopic, be used, the principal difficulty is to secure sufficient sap, in the event that the freezing temperature is determined by the Beckmann apparatus. The potato tuber satisfies this requirement in an excellent way. This paper is intended to present some of the results obtained in the study of the osmotic pressure of the sap taken from potato tubers kept at room temperature and in ice boxes. In this brief paper, there is no intention of giving a review of literature pertaining to the subject of osmotic pressure in its relation to after-ripening. The literature on after-ripening has been completely presented by Miss ECKERSON in a recent paper.[1]

Methods

In studying osmotic pressure in potatoes, an effort was made to reduce the experimental work to a single factor and that the limiting factor, heat. Various kinds of potatoes were used, such as the Burbank, Russet Burbank, Triumph, Snowflake, and Dakota Red. The potatoes were gotten in the autumn, wrapped in paraffine paper, and placed in two collections. One was buried in dry sand or gravel and kept at room temperature of 22–25° C.

[1] ECKERSON, SOPHIA, A physiological and chemical study of after-ripening. BOT. GAZ. 55:286–299. 1913.

The other potatoes were placed in a dark box and inclosed in an ice chest the temperature of which was 2–5° C. At different intervals specimens were taken from each collection, washed carefully, peeled so that considerable cortex was left with the central part of the potato, and then they were broken down with a glass scraper in a porcelain dish and the sap expressed from the potato pulp. This was tested in the Beckmann apparatus, the directions given by HAMBURGER in *Osmotischer Druch und Ionenlehre* being followed.

Procedure and results

The accompanying graphs indicate the readings at stated intervals. Graph 1 (fig. 1) shows the gradual rise of osmotic pressure in the ice box Burbank potatoes between the beginning and the close of the experiment, October 31, 1911, to January 23, 1912. At the latter date the pressure of the potato sap measured in atmospheres was 14.051. The pressure measurements of the sap in the room potatoes in this experiment ceased on December 5, when the osmotic pressure, measured in atmospheres, reached 7.4. During the progress of this work it seemed possible that filtration might prove interesting, consequently a set of tests with the filtered sap paralleled those made with the unfiltered sap. In most cases the readings of the unfiltered were higher than those of the filtered sap.

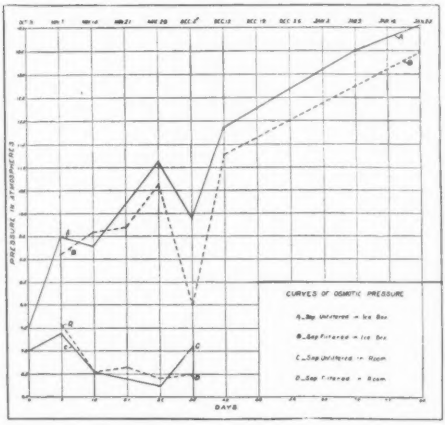


FIG. 1

The notable diminution in the pressure curve for December 5 was very difficult to account for at the time the reading was

made. Subsequently it appeared that it was largely due to the fact that small specimens were taken from the ice box on that date. The size of the potato is of such consequence that the potatoes should be selected for uniformity at the beginning of the experiment. What the causal agent is has not been determined, but it uniformly appeared in the various tests made with the different varieties used in these osmotic studies.

Graph 2 (fig. 2) contains a summary of the readings made in a set of experiments extending from January 22, 1912, to July 17, 1912. A pronounced lift in osmotic pressure in the sap taken from

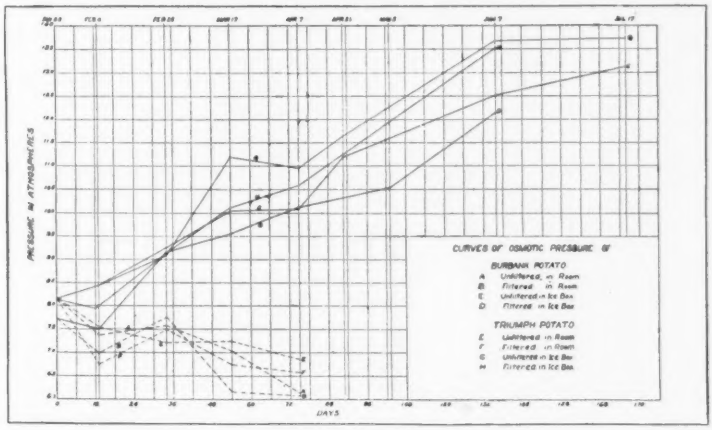


FIG. 2

the ice box potatoes is well illustrated, and the depression in the osmotic pressure in the sap taken from the room potatoes is also clearly shown. In the progress of this work there are certain interesting variations which seem to be related to the question of filtration of sap and also intimately associated with the size of the potatoes from which the sap was secured. As already noted, the curve for the unfiltered potato sap ran considerably higher on the average than that of the filtered. It was more pronounced in the case of the ice box potatoes than in those kept at room temperature. The filtered and unfiltered sap from ice box Burbank potatoes

showed a varying pressure ranging from 0.1 to 0.9 atmospheres. The Triumph ice box potatoes gave a somewhat larger variation when filtered and unfiltered sap collections were tested, one reading amounting to 1.08 atmospheres greater pressure in the unfiltered specimen.

The difference of pressure in the sap taken from a large and a small Burbank in the ice box ranged from 0.5 to 1.32 atmospheres, and in the case of sap obtained from a large and a small Triumph, kept in the ice box for 8 weeks, there were 1.69 atmospheres in favor of the larger specimen.

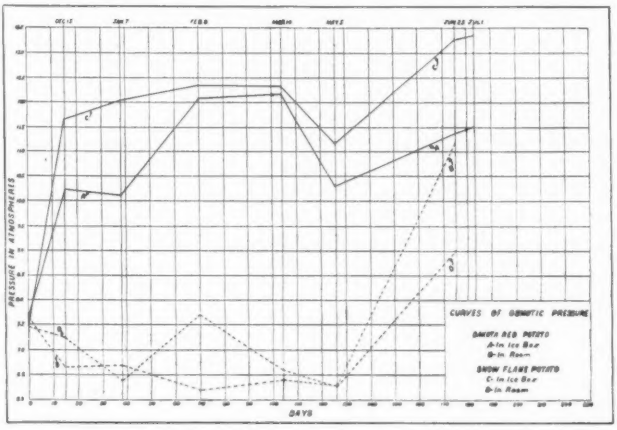


FIG. 3

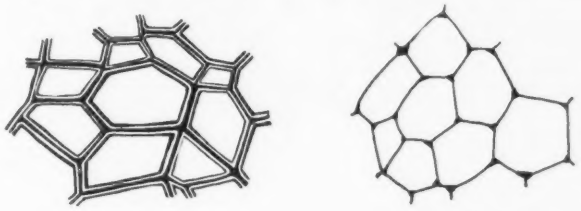
The third graph (fig. 3) represents the readings which have been taken in a study of the Dakota Red, which is a very large potato, and the Snowflake which is much smaller. This set of readings extended from October 31, 1912, to July 1, 1913. Again the rapid ascent of osmotic pressure in the potatoes kept in the ice box is clearly shown, whereas the osmotic pressure of those kept at room temperature declined.

The rapid lift in the curves *B* and *D* in the room temperature potatoes is associated with the loss of water which left these specimens and moved into young potatoes that were developed between

May 5 and July 1, and a consequent concentrating of the solutes in the sap which was expressed with great difficulty from the old, wrinkled potatoes kept 8 months in dry sand at room temperature.

In the last series of readings a comparison of filtered and unfiltered sap was not made in every case, but whenever the test was conducted the unfiltered sap showed somewhat greater pressure than the filtered.

The fact that the larger potatoes gave a higher osmotic pressure than smaller ones seems to hold only between those within a given variety. At any rate, in this last set of readings the Snowflake, which is a much smaller potato than the Dakota Red, gave a higher pressure. However, it was found that a small Dakota Red gave



a *b*

FIG. 4.—Tissue of potatoes 140 days after test began: *a*, Dakota Red potato at room temperature, with thick walls, ×136; *b*, ice box potato, with thin walls, ×136.

a lower pressure than a large Dakota Red kept under the same control conditions, and likewise that a small Snowflake gave a lower pressure than a larger Snowflake when they had been kept under the same control conditions.

It was observed in macerating the potatoes used in the readings recorded in this paper that the tissues of the ice box potatoes became increasingly more brittle with the lengthening of the experiment. The supply of free starch became reduced and the proportionate amount of water seemed to be increased. The room potatoes tested at the same time in the control work were found to have an increasing toughness as the time of the experiment extended. This result was clearly related to the cell-wall structure. The accompanying drawings (fig. 4) indicate why the tissues of the ice box potatoes broke down so much more readily under the macer-

ating tool than did the tissues of those kept at room temperature. In the former, no hemicellulose remains after 90–120 days. The drawings show the situation in the tissues of the room temperature potatoes and the ice box potatoes after a test of 140 days.

The chemical reaction of the tissues taken from the ice box and room temperature potatoes indicates a greater acidity in the former than in the latter. Furthermore, it shows that the acidity is greatest in the eye region, and that it gradually diminishes until it quite disappears as the distance from the eye into the cortex increases.[2]

Comparative tests of osmotic pressure in sap taken from the cortical part of the potatoes and from the vascular cylinder portions indicated that there was considerable difference in the sap taken from these regions in the same potatoes. There were minor variations noted which were easily within the range of error incident to the instrument and the indirect method employed in determining the osmotic pressure.

Conclusions

1. Heat is a limiting factor in controlling the processes which develop the substances that give rise to variation in osmotic pressure in potato sap.

2. Lowering temperature causes an increase in acidity, which in turn seems to be the controlling agent in the release of the enzymes which hydrolize starch and hemicellulose.

3. The carbohydrates hydrolized furnish the energy which is used by the potato while carrying on its metabolism during cold storage.

This work was undertaken at the suggestion of Dr. WILLIAM CROCKER to whom I am greatly indebted for much valuable assistance.

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[2] For the acid determinations I am indebted to Dr. SOPHIA ECKERSON.

THE CASTOR BEAN PLANT AND LABORATORY AIR

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 178

E. M. HARVEY

It is well known that the leaves of the castor bean (*Ricinus communis*) are likely to show nastic drooping after the plant has been brought into the laboratory. On account of the apparent definiteness of this response, it seemed probable that the plant would prove useful as a delicate test for certain gaseous impurities in laboratory air. It was with regard to this possibility that the studies reported below were undertaken.

Potted seedlings, grown under ordinary greenhouse conditions until they had developed 5–7 leaves, including the cotyledons, were used in the tests. The pots and soil were covered with paraffin to avoid absorption of the gases. Exposure periods were all approximately 60 hours. The methods of exposure to known concentrations of ethylene and illuminating gas were the same as described by KNIGHT and CROCKER[1] for these gases in their work on sweet pea seedlings. In the main, the 50–100-liter galvanized iron cans were used for exposure chambers, but, since here the plant would be in total darkness during the course of the experiment, some were exposed under bell jars provided with water seals and left in strong diffused light, in order to find what effect light would have on the sensitiveness of the response. Corresponding results, however, were obtained by the two methods. Illuminating gas tests were run parallel with those of ethylene in a manner to yield evidence whether the reaction was induced by the ethylene constituent of the illuminating gas. Ethylene occurs in the Chicago illuminating gas in the concentration of about 4 per cent, so pure ethylene was diluted with air to 4 per cent, so that, volume for volume, the illuminating gas and the ethylene-air mixture held about the same amount of ethylene. This stock mixture allowed parallel experiments to be carried out readily.

[1] KNIGHT, L. I., and CROCKER, W., Toxicity of smoke. BOT. GAZ. 55:337–371. 1913.

The reaction itself is very easily observed. The most obvious effect of the gas is the nastic drooping of the leaves as mentioned above. This drooping is brought about by curvatures, located either at the inner or at the outer end of the petiole or at both. If the gas be of certain concentration, the older leaves may develop abscission layers that often result in leaf fall. And again, if the gas be somewhat stronger, rapid proliferation may take place at these new leaf scars, forming small masses of tissue which usually exude sap. The most delicate response of the plant seems to be a nastic folding down of the laminae of the young leaves. However, the very young leaves that are still more or less enveloped by the bud scales seldom show any response.

Data regarding the appearance and degree of these responses were obtained by observation of the following points. Previous to the exposure, the leaves of the plant were numbered consecutively from cotyledons upward. Also the condition and direction of the plane of the leaves were noted. This consisted in an examination for abscission layers already started, the measuring of the angle made by each petiole with the stem, and the angle made by the plane of the leaf surface with the petiole. After exposure, examination was made for leaf fall, starting of abscission layers, the new angles made by the petioles with the stem and by the plane of the leaf surfaces with the petioles, and, finally, the condition of the laminae of the young leaves was noted. The amount of nastic drooping at each end of the petioles was recorded in degrees.

The results of the experiments proved that this plant has great capacity for response to low concentrations of ethylene, just as one was led to expect from its common behavior in the laboratory. The lowest concentration tried was one part ethylene to 10,000,000 of air (or 0.00001 per cent). With this amount the response was absolutely definite, as shown, for example, in one case by a nastic drooping of 15° at the inner end of the petiole for leaf no. 5; by drooping of 30° and 15° at the outer ends of the petioles for leaves nos. 5 and 6 respectively; and by a nastic folding down of laminae for leaves nos. 6 and 7. Parallel experiments with illuminating gas and ethylene, where the ethylene constituent of the former was about equal to the ethylene in the corresponding

ethylene-air mixture, gave results similar in kind and degree. This fact indicates that the ethylene of the illuminating gas is responsible for the reaction. Especially does this seem true in the light of similar results obtained by KNIGHT and CROCKER on sweet pea seedlings. The definiteness of the reaction with one part ethylene to 10,000,000 of air leads one to believe the plant

TABLE I

PLANT *A* EXPOSED TO 1 PART ETHYLENE TO 1,000,000 AIR; PLANT *B* EXPOSED TO 25 PARTS ILLUMINATING GAS TO 1,000,000 AIR (I.E., APPROXIMATELY 1 PART ETHYLENE TO 1,000,000 AIR); PLANT *C* THE CONTROL

Number of leaf	Plant	No response	Proliferation at leaf scar	Leaf fall	Starting of abscission layer	Nastic drooping of petiole; inner	Nastic drooping of petiole; outer	Nastic folding down of lamina of leaf
1 (cotyl.)	A	×						
	B				×			
	C	×						
2 (cotyl.)	A			×				
	B				×			
	C				×			
3	A	×						
	B						× 45°	
	C	×						
4	A					× 45°	× 45°	× (?)
	B					× 30°	× 60°	
	C	×						
5	A						× 45°	×
	B					× (?)	× 45°	×
	C	×						
6	A						× 90°	××
	B					× (?)	× 90°	××
	C	×						

×× = very strong response.

capable of responding to even considerably lower concentrations than any yet tried. The least delicate of the reactions, the proliferation and exudation at leaf scars, usually appears in concentrations of about one part ethylene to 50,000 of air; while leaf fall and especially the starting of abscission layers may appear in concentrations as low as one part ethylene to 500,000 of air, or even one part ethylene to 1,000,000 of air. The nastic drooping of the youngest well developed leaves and the folding down of the laminae of the young leaves are the responses one must depend on for extremely low concentrations.

The accompanying table (table I) will serve to show the method of recording the reactions, and also how close is the parallelism between the ethylene and the illuminating gas under the conditions of concentration named above.

In conclusion it may be stated that the castor bean plant has proved capable of giving an easily observed response to extremely small amounts of ethylene; and on account of this fact the plant seems particularly useful for the detection of harmful gaseous impurities[2] in the air of laboratories and greenhouses.

The writer gratefully acknowledges the many valuable suggestions of Dr. WILLIAM CROCKER.

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[2] It would not be of value for such gaseous impurities as are not active in inducing this response, but ethylene, though in small amounts, is probably the most harmful and generally present of any laboratory air impurity.

CURRENT LITERATURE

BOOK REVIEWS

The Bonn textbook[1]

For nearly twenty years the *Bonn textbook of botany* has been the most prominent text of college grade in the world, having enjoyed a wider circulation and having been translated into more languages than any of its competitors. The first edition appeared in 1894, STRASBURGER writing the morphology, NOLL the physiology, SCHENCK the cryptogams, and SCHIMPER the phanerogams. Of the four original authors, only SCHENCK remains, but they had already prepared five editions together, thoroughly establishing the book, before SCHIMPER died, a victim of his own restless researches. His place was taken by KARSTEN, who has not only maintained the high standard of his predecessor but has improved this part of the work with each successive edition. NOLL wrote the physiology for the first nine editions, and then died suddenly, in the prime of his physical and mental vigor. JOST took his place, and from this time physics and chemistry have been increasingly conspicuous in this portion of the work.

The heaviest loss of all was sustained in the death of STRASBURGER, who had been the dominating personality of the book and who had prepared the morphology for eleven editions. In the twelfth edition, dated April 1913, FITTING, who succeeded STRASBURGER at Bonn, has written the morphology. There is considerable change in arrangement, some change in subject-matter, and some change in wording, even when there has been no change in ideas. An admiring pupil and personal friend of the master-botanist of his time must be excused if he fails to find an improvement in this section of the book.

SCHENCK, the only survivor of the founders, has been throughout a reliable, consistent writer, steadily improving his contribution and refusing to be swayed by temporary flurries in his subject.

The excellent illustrations have always been a feature of Bonn texts. Some new figures have been added, and for the first time all figures have been credited to their respective authors.—CHARLES J. CHAMBERLAIN.

Goebel's Organography

A second edition of this work[2] is appearing and the first volume is already before us. The revision has been thorough, some features of the first edition

[1] FITTING, H., SCHENCK, H., JOST, L., und KARSTEN, G., Lehrbuch der Botanik für Hochschulen. 12th ed. 8vo. pp. viii+620. *figs. 782.* Jena: Gustav Fischer. 1913.

[2] GOEBEL, KARL, Organographie der Pflanzen. Erster Tiel, Allgemeine Organographie. 8vo. pp. x+513. *figs. 513.* Jena: Gustav Fischer. 1913. *M* 16; bound *M* 17.

having been abandoned and much new material with numerous figures having been added. There is a change of view in regard to leaf arrangement, and alternation of generations receives some attention. Naturally the relation between form and function, the inheritance of malformations, and the significance of juvenile stages are of interest to all botanists, and whether one agrees with the author or not, GOEBEL's account is stimulating and should put a needful restraint upon those who would blindly assign every such phenomenon to heredity and recapitulation.

The intimation, in the preface, that botanists have left the older fields of morphology needs a word of comment, for there are still some of us who feel as much interest in the problems of evolution, heredity, and phylogeny, as in seeing "the wheels go round." We welcome this book as a wholesome check. The morphologist whose principal interest is in phylogeny needs it, just as the experimental morphologist, whose principal interest is in something other than phylogeny, needs to know more about the structure and development of the objects upon which he is experimenting.

The second volume, dealing with special organography and containing the index, will be awaited with interest.—CHARLES J. CHAMBERLAIN

NOTES FOR STUDENTS

Osmotic pressures.—RENNER[3] has rendered a very important service to plant physiology by summarizing and subjecting to a critical analysis the literature of recent years dealing with the methods of calculating the osmotic pressure of solutions. All methods heretofore used by physiologists have been based on the assumption that an osmotic pressure of 22.4 atmospheres at 0° C. produces a freezing temperature of −1.85° C. But this depression of the freezing point, according to the physicists, is brought about when a mole of a non-electrolyte is dissolved in 1000 cc. of water; whereas physiologists have always made up their solutions as weight per cent solutions, or as molecular solutions in which enough water is used to make 1000 cc. of solution, but still assuming that the osmotic pressure of these more concentrated solutions is 22.4 atmospheres for undissociated salts. The discussion centers about the work of MORSE, FRAZER, and their co-workers, whose exact determinations have now shown clearly that such solutions must be made up in weight normal instead of volume normal concentrations in order to yield osmotic pressures agreeing with the gas laws. RENNER shows from calculations based upon the determinations of MORSE that there is a very close relation between depression of the freezing point and osmotic pressure. He claims indeed that all the disagreements in the literature between the results of the cryoscopic and plasmolytic determinations of osmotic pressure are traceable to the fact that the

[3] RENNER, O., Über die Berechnung des osmotischen Druckes. Biol. Centralbl. 32:486–504. 1912.

freezing point method uses weight normal, whereas the plasmolytic method uses volume normal solutions. He shows conclusively in his discussion that it is the plasmolytic method which has been in error.

The large error of the old method is illustrated by the cryoscopic measurement of a volume normal cane sugar solution. The depression of the freezing point is −2.66° C., which indicates an osmotic pressure of 32 atmospheres instead of 22.4 atmospheres. The excess pressure is due to the sugar being dissolved in less than 1000 cc. of water. A comparison of the pressures for 67 per cent cane sugar and 18.5 per cent NaCl as calculated from the volume normal and weight normal concentrations is very illuminating also. The NaCl solution contains 3.6 moles of salt, 50 per cent ionized, in a liter of solution; while the sugar solution contains only 2.6 moles, with no ionizing, per liter. The NaCl should develop a much higher pressure according to the plasmolytic method of estimating pressures; but adopting the method of MORSE, now shown to be correct, which demands equal quantities of solvent, we find that the NaCl is dissolved in 928 cc., the sugar in only 439 cc. of water. The relations of the two solutions are seen to be actually the reverse of what the plasmolytic method indicates. Owing to the dissociation of the NaCl, the solutions are really nearly isosmotic. These examples serve to show the unreliability of the plasmolytic determinations with volume normal solutions, and the necessity, despite their inconvenience, of using weight normal solutions in the future.

It is unfortunate that the physical chemists have not determined the osmotic pressure of saturated solutions by the cryoscopic method. While RENNER makes clear that at the concentrations thus far measured the freezing point determinations will give the correct osmotic pressure, it remains to be demonstrated that this holds for all concentrations whatsoever. The direct determinations by Lord BERKELEY and HARTLEY for concentrated sugar solutions exceed the measurements called for even by the MORSE-FRAZER method. At present, the reviewer believes that these direct measurements, recently confirmed by TROUTON, are the most trustworthy determinations we have for concentrated solutions. If the cryoscopic methods should yield results in agreement with the direct measurements at these same concentrations, and with saturated solutions of various salts, its universal application could be admitted. If it does not, then still further correction of the formula for calculating the osmotic pressure of solutions must be made. Every physiologist interested in the determination of osmotic pressures should by all means read RENNER'S excellent discussion.—CHARLES A. SHULL.

Paleobotanical notes.—ARBER[4] has described 44 species of plants from a coal-field in Gloucestershire, none of which are new to Great Britain. The

[4] ARBER, E. A. NEWELL, On the fossil flora of the Forest of Dean coal-field (Gloucestershire), and the relationships of the coal-fields of the west of England and South Wales. Phil. Trans. Roy. Soc. London B **202**:233–281. *pls. 11–13.* 1912.

contribution deals chiefly with stratigraphy, but a fact of botanical interest is that several species, including *Annularia galioides*, *Sphenopyllum majus*, *Lepidodendrom dichotomum*, and three species of *Sigillaria*, were found in a higher horizon (Upper Coal Measures) than known before in Great Britain.

Miss HOLDEN[5] has begun a series of contributions dealing with the anatomy of mesozoic conifers, the first one giving the results of a study of some Jurassic material from Yorkshire. The collection proved to contain some typically abietineous woods and some typically araucarian woods, but most of the woods were intermediate between the two. It is concluded that the character of these transitional woods corroborates the view that the Abietineae are the oldest conifers and that the araucarians have been derived from them. A remarkably strong statement is the following: "Comparative examination of living and fossil forms leads to the rejection of all criteria except cellulose bars of Sanio as an infallible test for tribal affinities."

Miss HOLDEN[6] has investigated a collection of lignite from some Middle Cretaceous beds of New Jersey. Most of the plants belonged to *Cupressinoxylon*, *Araucarioxylon*, and *Brachyoxylon*, and will be described later. In the present paper three types of *Pityoxylon* are described as new species: *Pinus protoscleropitys*, *Pityoxylon foliosum*, and *P. anomalum*. The first mentioned is probably the earliest form with all the characters of a modern hard pine, and the occurrence of such a pine as early as the Middle Cretaceous is thought to argue strongly for the great antiquity of the genus *Pinus*. *Pityoxylon foliosum* is probably the wood of *Prepinus*, all the leaves being borne directly on the main axis, and combining characters that are now separated in hard and soft pines. *P. anomalum* has a woody structure like that of *Prepinus*, but all the leaves are borne on short shoots.

THOMAS[7] has described a leaf from the Jurassic of Yorkshire which he thinks represents a new genus (*Eretmophyllum*) of Ginkgoales. The leaves differ from those of *Ginkgo* in being oblanceolate or linear, but approach those of *Ginkgodium* in outline; the leaves of the latter, however, are shorter and comparatively broader and are often deeply divided at apex. The most important distinction, however, is found in the venation.

SEWARD[8] has described some dicotyledonous leaves from the coal measures of Assam, which are probably Tertiary, although there are claims that they

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[5] HOLDEN, RUTH, Contributions to the anatomy of mesozoic conifers. I. Jurassic coniferous woods from Yorkshire. Ann. Botany **27**:533–545. *pls. 39, 40.* 1913.

[6] ———, Cretaceous Pityoxyla from Cliffwood, New Jersey. Proc. Amer. Acad. **48**:609–623. *pls. 4.* 1913.

[7] THOMAS, H. HAMSHAW, On some new and rare Jurassic plants from Yorkshire; *Eretmophyllum*, a new genus of Ginkgoalian leaf. Proc. Cambridge Phil. Soc. **17**: 256–262. *pls. 6, 7.* 1913.

[8] SEWARD, A. C., Dicotyledonous leaves from the coal measures of Assam. Records Geol. Survey India **42**:93–101. *pls. 17, 18.* 1913.

belong to the Cretaceous. Of course in the absence of fruits and seeds the determinations are not altogether satisfactory. In any event, the families thought to be represented, each by one to three species, are Magnoliaceae, Anonaceae, Fagaceae, Myristicaceae, Lythraceae, Moraceae, Rubiaceae, Guttiferae, Burseraceae, Anacardiaceae, Ericaceae, Dipterocarpaceae, and Ternstroemiaceae. If one can draw any conclusion from this showing, it is that the dicotyledonous series was represented practically throughout its present extent.—J. M. C.

Morphology of Calycularia.—CAMPBELL[9] has studied the rare Javanese liverwort *Calycularia radiculosa*, found in small quantities near Tjibodas. The plant is strictly dioicous, the males being decidedly smaller than the females. It perhaps more nearly resembles *Symphyogyna* than *Pallavicinia* (*Blyttia*), with which a comparison is made. The endophytic fungus common to so many liverworts is conspicuous. Two forms of apical cells are present: one is the cylindric-lenticular type found in *Pellia epiphylla;* the other is the cuneate type common to Marchantiales, *Sphaerocarpus*, and most Anthocerotales.

Branching of *Calycularia* he says, "seems to be a true dichotomy, but whether one of the branches retains the original apical cell or whether two new apical cells are developed was not investigated." In order to have true dichotomy, the original apical cell by equal division must give rise to two new apical cells. But if, on the other hand, the original apical cell is retained by one branch, the apical cell of the other branch must be formed from a segment of the original apical cell, and we have, not *true* dichotomy, but *apparent* dichotomy. Of course in most cases, whether we have true or simulated dichotomy makes little difference in the appearance of the adult plant.

The earliest stages of the antheridium were not studied, but apparently it develops like that of the majority of Jungermanniales. In the ultimate division of the spermatogenous cells a wall is formed. No trace of a "Nebenkörper" or "accessory body" was found. Archegonia are grouped on a rudimentary receptacle. The number of neck cells is various, the highest number found being eight. Occasionally a binucleate neck canal cell was found, showing that the neck is being shortened. In one archegonium neck canal cells were enlarged and closely resembled eggs. This seeming reversion to a more primitive type of archegonium seems to be widespread in bryophytes.

Early stages in embryogeny were not studied. The capsule has a relatively thick wall. The foot is the mushroom-anchor shape so common in liverworts. The spore mother cells are deeply lobed, as is characteristic of practically all Jungermanniales. The "quadripolar" spindle of FARMER was

[9] CAMPBELL, DOUGLAS HOUGHTON, The morphology and systematic position of *Calycularia radiculosa* Steph. Leland Stanford Junior Univ. Publ., Univ. Series, Dudley Mem. Vol. pp. 43–61. *figs.* 12. 1913.

noted, but occasionally a conspicuous bipolar spindle was seen. *Calycularia* therefore seems to be a suitable form for settling the FARMER-MOORE controversy, and it is greatly to be regretted that CAMPBELL'S material is so scanty. He thinks that *Calycularia radiculosa* should be made the type of a new genus intermediate between *Mörkia* and forms like *Makinoa* or *Pellia*.—W. J. G. LAND.

Embryo sac of Aglaonema.—CAMPBELL[10] has published a further study of the embryo sac and embryo of *Aglaonema*, the species investigated being *A. simplex* and *A. modestum*. Among the results are the following: the primary sporogenous cell develops the embryo sac directly; the first divisions in the embryo sac result in four free nuclei arranged in pairs, and only one of the micropylar nuclei divides, producing the synergids, the other without division becoming the egg nucleus; there is no nuclear fusion preceding endosperm formation and there are no definite antipodal cells; no evidence of fertilization was seen; the sac becomes filled with endosperm tissue; in embryo-formation the synergids remain intact, "and it sometimes looks as if they also contributed to the tissues of the embryo"; the embryo finally completely fills the sac, the body regions being differentiated at a late stage in the development. —J. M. C.

Sex in Onoclea.—Miss WUIST[11] has used *Onoclea Struthiopteris* in an investigation to determine whether the sex of the dioecious gametophytes is predetermined in the spore. Soil and solution cultures were employed, also different intensities of insolation. The work has extended through several years, so that the results are well established, the fundamental one being that the sex of the gametophyte is not predetermined in the spore. It was shown that the gametophyte is either monoecious or apparently dioecious according to its age and environment; for example, in younger cultures in soil 5 per cent of all the gametophytes were monoecious; in older cultures 15 per cent were monoecious. A striking result was that 90 per cent of the gametophytes which originally bore archegonia were induced later, by "favorable conditions of nutrition," to produce antheridia; while 5 per cent of the gametophytes which originally bore antheridia were induced later to produce archegonia. The "male tendency" appeared to be latent in all parts of the apparently female gametophyte. The effect of various cultures and the incidental responses of various kinds are very suggestive.—J. M. C.

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[10] CAMPBELL, D. H., The embryo sac of *Aglaonema*. Scottish Bot. Review **1**:110–115. *pls. 1–4.* 1912.

[11] WUIST, ELIZABETH DOROTHY, Sex and development of the gametophyte of *Onoclea Struthiopteris*. Physiol. Researches **1**:93–132. *figs. 15.* 1913.